Behavioural ecology of Przewalski horses (*Equus przewalskii*) reintroduced to Hustai National Park, Mongolia

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Abstract

Studies on the behavioural ecology of Przewalski horses (*Equus przewalskii*) recently reintroduced into Hustai National Park, Mongolia were carried out between 1998 and 2000. Home range size and habitat use, social, marking, and vigilance behaviour, and their reaction to flies were quantified.

Home ranges of harems ranged from 129 ha to 2399 ha, with core areas of between 61 ha and 1196 ha. There was no relationship between range size and harem size, or length of time since release. The more nutritious vegetation at lower elevations was preferentially selected. The horses rested near ridges during the hotter parts of the day where there were fewer flies, and grazed in the valleys in the mornings and evenings. Woodland areas were used to shelter from the sun, despite their high fly abundance. Muscid flies were most frequently caught; Tabanids were rare.

Dominance was related to age, aggression and length of time in the harem. The frequency of associative behaviours did not correlate with any social factor, but had a hygienic function. Stallions marked stud piles and mare eliminations in different ways suggesting different functions. In addition to being vigilant for predators, the horses appeared to scan for social cues and food patches.

Home range size and habitat use, and general pattern of marking and vigilance behaviour, of the wild Przewalski horses were similar to those seen among feral domestic horses, although they tended to be less aggressive than captive and feral horses. So far, the re-establishment of Przewalski horses into HNP appears to have been successful, although constant monitoring of the population is necessary. As the population grows, there will be potential problems to do with exceeding the carrying capacity of the park and hybridisation with domestic horses. The future management of the horses is discussed.

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Contents

Abstract 2

Acknowledgements 3

Contents 4

List of tables 9

List of figures 12

List of plates 14

Chapter 1. Introduction 15

1.1 Introduction 16

1.2 Reintroductions 16

1.3 The Przewalski horse 20

1.3.1 Description 20

1.3.2 History 22

1.3.3 Reintroduction efforts 26

1.4 Home range and habitat use 28

1.4.1 Social organisation 28

1.4.2 Home range 31

1.4.3 Time budget 33

1.4.4 Vegetation use 35

1.5 Social behaviour 37

1.5.1 Agonistic behaviour 37

1.5.2 Associative behaviour 39

1.5.3 Marking behaviour 41

1.5.4 Vigilance behaviour 42

1.6 Effects of flies 44

1.7 Aims 46

Chapter 2. Methods 47

2.1 Study site 48

2.2 Study animals 48

2.2.1 Harem composition and changes 50

2.2.1.1 Khaan 50
2.2.1.2 Paritet 53
2.2.1.3 Bayan 53
2.2.1.4 Margad 54
2.2.1.5 Ares 54
2.3 Behavioural observations 54
2.3.1 Scan sampling 55
2.3.1.1 Ten minute scan sampling – Home range and habitat use 55
2.3.1.2 Bite rate 57
2.3.1.3 One minute scan sampling 57
2.3.1.3i Associative behaviour 57
2.3.1.3ii Vigilance behaviour 58
2.3.2 All-occurrence sampling 61
2.3.2.1 Agonistic behaviour 61
2.3.2.2 Marking behaviour 63
2.3.3 Fly sampling 63
2.3.3.1 Fly traps 63
2.3.3.2 Fly count 64
2.4 Data analysis 64
2.4.1 Home range and habitat use 65
2.4.2 Time budget 65
2.4.3 Vegetation use 66
2.4.4 Agonistic behaviour 68
2.4.5 Associative behaviour 71
2.4.6 Marking behaviour 71
2.4.7 Vigilance behaviour 71
2.4.8 Fly data 72

Chapter 3. Home range and habitat use 73
3.1 Introduction 74
3.1.1 Home range 74
3.1.2 Time budget 77
3.1.3 Vegetation use 80
3.2 Results 83

3.2.1 Home range 83
3.2.1.1 Range shifts between the years 89
3.2.1.2 Overlap between the ranges of different harems 93
3.2.1.3 Use of the home range 96
3.2.2 Time budget 100
3.2.2.1 Effect of time 100
3.2.2.1a Grazing 101
3.2.2.1b Stand resting 103
3.2.2.1c Standing 103
3.2.2.1d Moving 103
3.2.2.1e Recumbent rest 104
3.2.2.2 Effect of age and sex 104
3.2.2.3 Effect of other factors on the time budget 106
3.2.2.4 Synchronisation of behaviour 106
3.2.3 Vegetation use 108
3.2.3.1 Seasonal use of vegetation 114
3.2.3.2 Bite rate 114
3.3 Discussion 116
3.3.1 Home range use 116
3.3.2 Time budgets 119
3.3.3 Vegetation use 122
3.4 Summary 124

Chapter 4. Social behaviour 125
4.1 Introduction 126
4.1.1 Social structure of harems 126
4.1.2 Agonistic behaviour 127
4.1.3 Associative behaviour 129
4.1.4 Marking behaviour 131
4.1.5 Vigilance behaviour 132
4.2 Results 134
4.2.1 Rationale 134
4.2.2 Agonistic behaviour 134
4.2.2.1 Frequency of aggressive acts 134

4.2.2.2 Effect of age and sex on aggression 137
4.2.2.3 Retaliatory and defensive behaviour 138
4.2.2.4 Dominance hierarchies 142
4.2.2.4a Paritet's harem 145
4.2.2.4b Bayan's harem 146
4.2.2.4c Margad's harem 147
4.2.2.4d Khaan's harem 147
4.2.2.4e Ares' harem 147
4.2.2.5 Factors affecting dominance 148
4.2.3 Associative behaviour 148
4.2.3.1 Frequency of associative behaviour 148
4.2.3.2 Mutual grooming 150
4.2.3.3 Stand resting together 152
4.2.4 Marking behaviour 155
4.2.4.1 Frequency of marking behaviour 155
4.2.4.2 Stud piles 160
4.2.5 Vigilance behaviour 165
4.2.5.1 Frequency of vigilance behaviour 165
4.2.5.2 Vigilance according to age and sex 167
4.2.5.3 Stimuli causing vigilance 169
4.2.5.4 Vigilance of individual horses 169
4.3 Discussion 172
4.3.1 Agonistic behaviour 172
4.3.2 Associative social behaviour 176
4.3.3 Marking behaviour 179
4.3.4 Vigilance behaviour 180
4.4 Summary 184

Chapter 5. Effects of flies 186
5.1 Introduction 187
5.1.1 Biology of flies 187
5.1.2 Effect of flies on their host 190
5.2 Results 193
5.2.1 Species abundance 193

5.2.2 Spatial distribution 195
5.2.2.1 Trap data 195
5.2.2.2 Count data 195
5.2.3 The influence of environmental conditions on fly abundance 197
5.2.4 The effect of flies on Przewalski horses 199
5.3 Discussion 201
5.4 Summary 205

Chapter 6. Conclusions 206
6.1 Key findings 207
6.2 Management and future concerns 211
6.3 Applications for other reintroductions 214

References 216

Appendix 234

List of tables

1.1	Examples of previous mammal reintroductions	17
1.2	Species and subspecies of the genus Equus extant in the 20th Century	29
2.1	Studbook details of horses studied at HNP	51
2.2	Free ranging harems in HNP	52
3.1	Size and use of equid home ranges in the literature	75
3.2a	Time of day when various behavioural activities occur	78
3.2b	Proportion of a day spent in various behavioural activities	79
3.3	Vegetation use by different populations of feral horses, and populations of Przewalski horses, mountain zebras and feral asses	81
3.4	Difference in size between two home range methods: Minimum Convex Polygon (MCP) and the Kernel method	84
3.5	Sizes of home ranges and harems released in HNP between 1994 and 1998	84
3.6	Range shifts of home ranges and core areas within a harems range expressed as a percentage of the overlap in each year	90
3.7	Distance from the centre of the home range in one year to the centre in all other years since release	93
3.8	Overlap of home ranges and core areas between harems expressed as a percentage of the area covered in each year	94
3.9a	Daily time budgets of each harem	101
3.9b	Daily time budgets of each harem pooled over the years they were observed	101
3.10	Correlation between factors potentially affecting the time budget	106
3.11	Vegetation classes at HNP according to landscape features and dominant plant species	109
3.12	Habitat (vegetation) selection indices (w_i)	112

3.13	Habitat (vegetation) selection indices (w_i) in different seasons of the year	115
4.1	Frequency of aggression of each harem in each year	134
4.2	Aggressive behavioural elements observed in the different harems	136
4.3	Aggressive acts according to age and sex, when justified for number of animals	136
4.4	Retaliatory and defensive behavioural elements observed in the different harems, excluding fights among stallions.	141
4.5	Retaliatory and defensive behaviour observed from the different ages and sexes in each harem over all years	141
4.6	Results of Chi-squared tests for aggression received	142
4.7	Values for the linearity of the dominance hierarchies within harems	143
4.8	Direction of aggression within a harem	145
4.9	Elements of agonistic behaviour directed up and down the hierarchy	145
4.10	Associative interactions between ages and sexes	150
4.11a	Pearson's correlation coefficient between mutual grooming frequency and length of tenure in the harem, age or aggression in each harem	154
4.11b	Without the stallion in the analysis	154
4.12a	Spearman's rank correlation coefficient of stand resting together and length of tenure in the harem, age or aggression in each harem	154
4.12b	Without the stallion in the analysis	154
4.13	Sequence of behaviours when marking	160
4.14	Median dimensions of stud piles of different ages	160
4.15	Position of stud piles relative to the home ranges of the harems	161
4.16	Median frequency of vigilance of each harem	165
4.17	Vigilance of each age and sex	169
4.18	Spearman's rank correlation of various factors affecting vigilance	171
5.1	Families of Diptera in which one or more species parasitise mammals	188
5.2	Flies caught in traps in HNP, 1999	194
5.3	Diversity and evenness of types of fly at different trap areas	195

5.4	Per cent of flies found at different sampling areas per horse and per trap	195
5.5	The median value of the number of flies horse-1, temperature and wind speed at different areas used by the horses	196
5.6	Mean numbers of flies on horses of different colours	197
5.7	Per cent of flies on different parts of the horses body	197
5.8	Mean number of flies on a horse at different levels of comfort behaviour	199
5.9	Activity of the harems at different levels of comfort behaviour	200

Appendix I	Composition of free ranging harems at HNP	234
Appendix II	Sampling sessions and their division into standard days	240
Appendix IV	Results of Kruskal-Wallis analyses of time budget data of each harem	244
Appendix V	Amount of time behaviour is synchronous (%)	245
Appendix VI	Habitat (vegetation) selection indices	246
Appendix VII	Results of chi-square tests to show differences in use of different vegetation classes	250
Appendix VIII	Agonistic behavioural elements according to age and sex	251
Appendix IX	Dominance hierarchy matrices	253
Appendix X	Pearson's correlation coefficients and their significance for factors affecting the dominance of horses within each harem	257
Appendix XI	Flies caught in sticky and water traps, 1998	259
Appendix XII	Pearson's correlation coefficients between different environmental variables affecting the number of flies on a horse	259

List of figures

2.1	Hustai National Park	49
3.1a	Size of the home range and core area of harems since release	85
3.1b	Home range size of harems composed of different numbers of horses	85
3.2	Distribution and overlap of home ranges at HNP from 1995 to 2000	86
3.3	Overlap within home ranges 1995 - 2000	91
3.4	Mean size of home ranges (1995 – 2000) in the different seasons	97
3.5	Seasonal use of the home range	98
3.6	Use of the home range at different temperature conditions	98
3.7	Hourly time budget of all harems pooled over all years	102
3.8	Monthly time budget of all harems pooled over all years	102
3.9	Differences in the mean frequency of activity of the different ages and sexes of Paritet, Bayan and Margad's harems, 2000	105
3.10	Effect of number of horses in the harem and time since release on grazing and stand resting behaviour	107
3.11	Vegetation classes in the home ranges of harems in HNP	110
4.1	Behavioural elements observed during aggressive acts	135
4.2	Aggressive acts elicited and received by the different ages and sexes	137
4.3	Agonistic behaviour elements used by each age and sex	139
4.4	Behavioural elements observed during retaliatory or defensive behaviour	140
4.5	Correlation coefficients of aggression, age and length of time in the harem with position in the dominance hierarchy	149
4.6	Associative behaviours seen in the horses at HNP	151
4.7	Parts of the body observed mutual groomed	151
4.8	Effect of hour and month on mutual grooming and stand resting together	153
4.9	Observations of marking events in each month	156
4.10	Stimuli marked in each month	156
4.11	Pattern of marking behaviour	157

4.12	Dimensions of stud piles	161
4.13	Position of all stud piles observed marked by the stallions and their home ranges	162
4.14	Placement of stud piles	164
4.15	Frequency of vigilance behaviours	166
4.16	Box plots to show the frequency of vigilance in each month	167
4.17	Box plots to show the frequency of vigilance across the hours of the day	168
4.18	Stimuli causing vigilance	170
5.1	Graphs to show the similar effects of fly abundance on the comfort behaviour of ridden horses and Przewalski horses	198
Appendix III	Utilisation curves of the different harems	243

List of plates

1.1	Different colours of Przewalski horses	21
1.2	Characteristic features of the Przewalski horse	21
1.3	Cave painting of a horse similar to a Przewalski horse	23
1.4	Map of Mongolia	23
2.1	Buyana and Naidvar mutual grooming	59
2.2	Stand resting together	59
2.3	Different levels of vigilance	60
2.4	Mild bite threat evoking a large response	62
2.5	Margad herding	62
3.1	Resting among trees	99
3.2	Resting by rocks	99
4.1	Sequence of marking a stud pile	159

Chapter One

Introduction

Chapter 1. Introduction

1.1 Introduction

This study set out to examine the behavioural ecology of Przewalski horses (*Equus przewalskii*) reintroduced to Mongolia. Nothing was known about the natural biology of these animals because they became extinct in the wild before they could be studied. Almost all previous research has been carried out on captive populations. Therefore, studies of these reintroduced animals can provide information that will aid the future management of the horses, and will generally be relevant to other wild equids and other animals. There are few publications presenting the full results of reintroductions, and reviews of reintroduction success have cited the importance of research of animals post-release (e.g. Fischer & Lindenmayer, 2000; IUCN, 1995). The results of this study therefore should also be relevant to future reintroductions.

1.2 Reintroductions

Reintroductions are lengthy, complex and expensive processes (IUCN, 1995), yet approximately 27% of the 116 reintroductions over the past 20 years have been classified as failures. A further 47% of reintroductions have had an unknown success rate (Fischer & Lindenmayer, 2000). Up to 1989, Kleiman (1989) reported that 50% of the 1000 cases of bird reintroductions, and about 75% of the 20 mammal reintroductions had failed. Despite this, the number of reintroductions or translocations each year is increasing; the average number per year doubled between 1974 and 1981 (Griffith *et al.*, 1989), and has increased from nine reintroduction attempts reported in the literature of the 1970s to 60 in the 1990s (Fischer & Lindenmayer, 2000). It is therefore very important to examine what makes some reintroductions successful in order that this information can be used to help future efforts (Fischer & Lindenmayer, 2000; Seddon, 1999; Wolf *et al.*, 1998). Examples of mammal species that have been reintroduced are given in Table 1.1.

Table 1.1. Examples of previous mammal reintroductions.

Species	Country of release	Reference
Ungulates		
Arabian oryx (*Oryx leucoryx*)	Oman	Stanley Price, 1991
Mountain gazelle (*Gazella gazella*)	Saudi Arabia	Dunham, 2000
Asiatic wild ass (*Equus hemionus*)	Israel	Saltz *et al.*, 2000
Bighorn sheep (*Ovis canadensis*)	USA	Osterman *et al.*, 2001
Carnivores		
Black footed ferret (*Mustela nigripes*)	USA	Biggins *et al.*, 1999
Otter (*Lutra lutra*)	Sweden	Sjoasen, 1996
Red wolf (*Canis rufus*)	USA	Moore & Smith, 1990
Grey wolf (*Canis lupus*)	USA	Bangs & Fritts, 1996
Swift fox (*Vulpes velox*)	Canada	Herrero *et al.*, 1986
Rodents		
Red squirrel (*Sciurus vulgaris*)	UK	Venning *et al.*, 1997
Primates		
Golden lion tamarin (*Leontopithecus rosalia*)	Brazil	Kleiman, 1989
Marsupials		
Burrowing bettong (*Bettongia lesueur*)	Australia	Short & Turner, 2000

The IUCN (1995) set up guidelines to aid the growing number of reintroduction projects. They define reintroduction as, "an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct". Reintroduction can be carried out for a variety of reasons: as part of a comprehensive conservation effort for a species that includes habitat restoration and public education; to manipulate the genetic or demographic composition of a population; or to repopulate an area where the species has been extirpated (Kleiman, 1989). The Przewalski horse has been reintroduced for a combination of all these reasons. Ultimately, success can be defined as survival of the release generation, breeding by the release generation and their offspring, and persistence of the re-established population (Seddon, 1999). However other studies have set different qualifications for success, such as breeding by the first wild-born generation, a three year breeding population with recruitment exceeding loss, a total population figure, or the establishment of a self-sustaining population (Seddon, 1999). These qualifications will partly depend on the animal released. In the case of the burrowing bettong (*Bettongia lesueur*) the criteria for success were persistence of the population for more than five years, and for the population to contain more than 265 animals within that time (Short & Turner, 2000). In this case these criteria were met, although 'success' as an end point is an illusion. For example the reintroduction of the Arabian oryx (*Oryx*

leucoryx) to Oman was considered to be a success, but twenty years after the first animal was released poaching has made the population no longer viable (Seddon, 1999).

Captive breeding, with an ultimate aim of reintroducing a species, is increasingly part of the conservation effort for endangered or threatened species (Conway, 1980). However there is a danger of keeping animals in zoos for too long before release. Although most endangered species are now carefully managed by stud books to reduce the effects of inbreeding, within zoos there is likely to be a process of loss of genetic variability by domestication (Foose, 1986; May, 1991; Ryder, 1986), as animals best able to cope with captivity are more likely to breed (Price, 1999). There was therefore the danger that animals like the Przewalski horse, that have been entirely captive bred for 13 generations, would be unable to survive in the wild (Klimov & Orlov, 1982).

Each reintroduction is an experiment (May, 1991), but there are now some successful reintroductions whose lessons can be learned. Griffith *et al.* (1989) found that translocated threatened, endangered or sensitive species had a lower success than native game, although this was not found to be a factor in other studies of reintroduction success (Fischer & Lindenmayer, 2000; Wolf *et al.*, 1998). However all studies found that translocations of wild caught animals were more successful than captive raised ones (Fischer & Lindenmayer, 2000; Griffith *et al.*, 1989; Wolf *et al.*, 1998). This was shown by Sjoasen (1996), who found that wild caught otters (*Lutra lutra*) had almost twice the survival rate of those captive bred after one year. Predation of wild animals has often been observed to be less than for captive born animals (Price, 1999).

It is important for animals that are chosen for reintroduction to have the skills necessary for survival (Konstant & Mittermeier, 1982). It is possible to teach anti-predator behaviour, as mortality from predation is a risk when reintroducing captive bred animals (Griffin *et al.*, 2000). Survival skills can also be 'taught' at least partly by environmentally enriching the enclosure in which the animals are kept in captivity (Box, 1991). In the case of the red lion tamarin (*Leontopithecus rosalia*) this involved teaching the tamarins to forage by gradually replacing a single bowl of food with food distributed throughout the enclosure and hidden, so the animals had to work to get it (Kleiman, 1989). For ungulates, preparation for a natural diet can be as simple as providing appropriate natural forage instead of concentrated food. There is then a

definite need for acclimatisation to the new environment at the release site, and in the case of social animals, to the other members of the new group prior to release (May, 1991). Small enclosure size and lack of acclimatisation time appeared to be factors affecting the mortality of translocated squirrels (*Sciurus vulagaris*) after some releases in Britain (Venning *et al.*, 1997).

Przewalski horses for release in Hustai National Park were chosen partly as a result of the way that they had been kept in captivity (Bouman, 1998). Horses that have spent time in a group with conspecifics and have lived on grass are likely to do better than those that have been kept alone or in a dirt enclosure. A Przewalski stallion that had been kept in a dirt floored enclosure had to be taught to graze grass for three weeks before he could be introduced to a reserve in France. The other horses, which had been raised on pasture, needed no learning period (Feh & Carton de Graumont, 1995). Foraging behaviour is a key skill for herbivores and using animals with this experience will help their success when reintroduced (Tear & Ables, 1999). Selecting horses from very large grassy enclosures with little or no contact with humans should combine the benefits of using captive bred animals (which will be in better condition and individuals can be chosen more easily, or the whole group can be taken if desired) with that of translocated wild caught animals (which are likely to be more wary of humans and not reliant on them for food) (Gordon, 1991). As reintroduction is a stressful situation (Saltz & Rubenstein, 1995), success is more likely using animals that are better able to cope with new experiences, and that have at least basic experience of their future environment (Box, 1991).

Two studies found that animals reintroduced to their historic range were more successful than those introduced to the periphery or outside of it (Griffith *et al.*, 1989; Wolf *et al.*, 1998), although Lomolino and Channell (1998) argued that endangered mammals often persist along the edges of their historic range, as these are areas where there are fewer anthropogenic disturbances, and often have a more diverse habitat and environmental conditions. There is debate as to whether Hustai National Park is actually part of the historic range of the Przewalski horse (van Dierendonck & Wallis de Vries, 1996). However to a certain extent it appears that this depends on how far back the history of the species is taken. Przewalski horse-like animals were seen on Mammoth Steppe in prehistoric times, which consisted of habitat similar to modern Eurasian steppe (van Dierendonck & Wallis de Vries, 1996). The situation is further confused by the paucity of records of sightings of the species before the 19th Century

and the fact that it is difficult to distinguish the few fossil remains from those of domestic horses (Bouman & Bouman, 1994). When reintroduction is considered, the quality of the habitat, which appears to be good at Hustai National Park, is an important factor for success, having an effect regardless of how many animals are released and how well prepared they are (Fischer & Lindenmayer, 2000; Griffith *et al.*, 1989; Wolf *et al.*, 1998).

It appears that, in general, ungulate reintroductions are less problematic than those involving other taxa, probably because they are relatively resilient in their requirements and adaptable to novel stimuli (Gordon, 1991). Domestic horses (*Equus caballus*) appear very adaptable and are found in feral form in a great variety of habitats (Linklater, 2000). There have been several other successful reintroductions of ungulates, in particular to arid areas, such as the famous reintroduction of the Arabian oryx to Oman. These reintroductions show the importance of long term studies of a new population. Tear and Ables (1999) found that the whole social system of the oryx changed as forage conditions deteriorated after rain. If the oryx had only been studied for the first four years (until the rain fell) a totally different idea of their social system would have been obtained than subsequently proved to be the case (Tear & Ables, 1999). A population of Asiatic wild ass (*Equus hemionus*) had low reproductive success for the first five years after release, initially causing a slower rate of increase of the population than might have been expected (Saltz & Rubenstein, 1995). Especially in the case of animals that have not previously been studied in the wild, or that have been kept in captivity for many generations, such as the Przewalski horse, long term studies are vitally important to show changes in the demography and behaviour of the population.

1.3 The Przewalski horse

1.3.1 Description

The Przewalski horse, or takh in Mongolian, is generally a tan brown colour, which can range from a pale cream in some animals to a deep brown in others (Plate 1.1). The head and neck is normally darker than the body, and the belly and inside of the legs are lighter. A dorsal stripe runs from the mane to the tail and stripes are often seen on the legs at the back of the knee and hock (Plate 1.2). Przewalski horses have

Plate 1.1. Different colours of Przewalski horses.

Plate 1.2. Characteristic features of the Przewalski horse – erect mane, dorsal stripe, stripes on legs and short dock hairs.

an erect mane with no forelock that is dark brown to black and often has shorter, lighter hairs growing along each side. The tail of the Przewalski horse is also dark brown or black and, unlike the domestic horse, the proximal region of the tail has shorter, lighter coloured hairs and then the hairs get longer and darker distally, grading into the long dark tail hair (Groves, 1994).

Ten Przewalski horses that were first or second generation from the wild and more than three years old were measured in Askania Nova. Of these, six males stood 138 to 146 cm, and four females were 134 to 140 cm high at the withers (Groves, 1994). Przewalski horses have a stocky build with a low-slung, thick neck and short but slender limbs. They have a short and high muzzle and a straight lower margin of the jaw. This results in the dorsal profile of the head having an angle of about 20°, whereas in domestic horses it is 25°-30° (Mohr, 1971).

Although Przewalski horses can interbreed with domestic horses they have a different number of chromosomes. Przewalski horses have 2n = 66 chromosomes whereas domestic horses have 2n = 64, thus the two species are more different than any two breeds of domestic horse (Ryder, 1994). Hybrids are fully fertile and have 2n = 65 chromosomes.

1.3.2 History

The last authenticated sighting of a Przewalski horse in the wild was by a Mongolian scientist in 1969 by the Tachyn-shar mountains in the western Gobi (near the Mongolian-Chinese border) (Bouman & Bouman, 1994), and it is now likely that they are extinct throughout their former range. In the mid-Pleistocene (1 million years ago) species of *Equus* arose in North America and migrated across the Bering land bridge to disperse over most of the Eurasian land mass (Simpson, 1961). Pictures of horses are found in caves in Italy, France and Spain dating from about 20,000 years ago (Bouman & Bouman, 1994). These horses have the same erect mane, lack of forelock and colouring as the Przewalski horse (Plate 1.3). Although they cannot be said to be the same species, these paintings show that similar animals once ranged throughout Eurasia. After the last ice age around 10,000 years ago there were three types of horse in Eurasia which appear to have been geographically separated. The Przewalski horse was present in Asia, and the steppe tarpan, *Equus ferus*, and forest tarpan, *Equus przewalskii silvaticus*, occupied the steppes and forests of western Russia and eastern Europe (Groves, 1994). The last of the tarpans died in 1918, but they have since been

Plate 1.3. Cave painting of a horse similar to a Przewalski horse. Lascaux caves, France.

Plate 1.4. Map of Mongolia. The two reintroduction sites are marked. The star marking HNP obscures the word 'Töv', the name of the aimag (province).

reconstituted from similar looking domestic breeds and used as a grassland management tool. The actual number of ancient sub-species of horse and their distribution is not well known as their fossils are hard to tell apart (Waring, 1983). Domestication began about 3,000 BC and this makes things more confusing. It is likely that wild horse populations were reduced by absorption into domestic stock, or were extirpated because they damaged crops and stole domestic mares (Waring, 1983).

It is still unclear whether *Equus caballus*, the modern domestic horse, is derived from the Przewalski horse, or whether there is no direct ancestral relationship. Mitochondrial DNA analysis suggests that there is a more ancient genetic divergence between the two species than would be expected if the Przewalski horse was the progenitor of the domestic horse, but more research is needed before full conclusions can be drawn (Ryder, 1994). With the advent of the domestic horse in the fossil record it is hard to follow the history of the Przewalski horse, but it is likely that they were gradually restricted to the central Asian steppes and semi-arid deserts by the growing human population (Bouman & Bouman, 1994).

Przewalski horses first became known to western science in 1878. Colonel Nikolai Przewalski made several expeditions to central Asia for the Russian Czar Alexander the Second, and at the Chinese-Russian border post on the return from one such trip he was given the skull and hide of a horse (Bouman & Bouman, 1994). He took these to Poliakov at the Zoological Museum in St. Petersburg where they were confirmed as the remains of a wild horse and the species was given the name *Equus przewalskii* Poliakov, 1881. There had been sightings of 'wild horses' before this time ranging from writings of a Tibetan monk in 900 AD to the horses that apparently caused Chinggis Khaan's horse to rear and throw him to the ground in 1226 (Bouman & Bouman, 1994). However it is hard to be certain whether some observations refer to Przewalski horses, or simply escaped domestic horses or wild asses (*Equus hemionus*). All sightings within the last 200 years occurred within the relatively small area around the current Chinese-Mongolian border (85-95°E, 44-50°N) (Mohr, 1971) and it was here that all Przewalski horses were subsequently captured.

By the end of the Nineteenth Century efforts were being made to bring Przewalski horses to European zoological collections. The first Przewalski horses were caught in 1899, of which five survived and were taken to Askania Nova, a large estate in the Ukraine. Between 1900 and 1903 more horses were caught; 40 survived and were sent

to zoos in Europe and America. Since then only two horses are known to have been caught. One mare, caught in 1938, was kept in Mongolia and another mare, Orlitza III, was caught in 1947 and sent to Askania Nova (Bouman & Bouman, 1994). Orlitza III was subsequently very important for her input to the genetic stock of the captive population.

It is likely that Przewalski horses were already quite rare in the wild in the first half of the 20th Century, with only occasional sightings of small groups of horses being reported (Bouman & Bouman, 1994). There are many factors that could have caused the extirpation of the horse after the Second World War, and it is likely that it was a combination of these acting on a small population that caused their extinction. One major factor affecting the horses was the change in the political climate of the area. In the 1940s and 1950s modern weapons became more abundant in the region and, with the lapse of Buddhism in Communist Mongolia, there was no taboo against shooting more animals than were needed. In addition, Kazakhs were allowed to settle the area and these people relied heavily on hunting for food (Bouman & Bouman, 1994). In the 1950s the border post between Mongolia and China was moved, providing the local herdsman access to grazing and springs that until then had only been used by the wildlife. There were also a series of very harsh winters in the 1940s and 1950s causing the deaths of large numbers of livestock and undoubtedly had a large effect on the already small population of Przewalski horses (Bouman & Bouman, 1994). Finally the Przewalski horse is likely to have become extinct as a species due to hybridisation. One case of a Przewalski stallion acquiring a harem of domestic Mongolian mares is known (Mohr, 1971), and it is likely there were more. It has been found in the red wolf (*Canis rufus*) that when the wild population became small, and when reintroduced to North Carolina, dispersing young wolves mated with coyotes if they could not find conspecifics (Moore & Smith, 1990). As the Przewalski horse population became small it would not have been difficult for them to become assimilated into local herds of domestic horses.

Between the first captures in 1899 and 1935 the Przewalski horse did not breed very well in zoos, and this resulted in only twelve known Przewalski horses, and one domestic horse (maybe more), forming the founders of the subsequent captive population (Bouman & Bouman, 1994). After the Second World War the captive Przewalski horse population went through another bottleneck as only nine of the thirty-one horses that survived the war bred. Until the1970s Przewalski horses tended

to remain in the same zoos and there were many instances of consanguinous matings, causing the level of inbreeding to rise sharply in most collections (Bouman & Bouman, 1994). Some genetic diversity was lost due to the small population size and there was evidence of inbreeding depression causing the population to grow more slowly than its potential (Ryder, 1994). To ameliorate this a Species Survival Plan was set up for the Przewalski horse in the USA in 1979, and this was followed in 1986 by a European breeding programme, or EEP (Europaisches Erhaltungszucht-Programm) (Bouman & Bouman, 1994). These programmes led to a greater exchange of animals between zoos with efforts being made to reduce inbreeding and increase or maintain genetic diversity by ensuring that all the founders were represented in the captive population. By the 1990s there was a population of nearly1500 Przewalski horses in captivity and plans were being made for their reintroduction.

1.3.3 Reintroduction efforts

The Przewalski horse was never studied properly in the wild and so only anecdotal accounts of its social structure and behaviour are available (Mohr, 1971). There have been only two efforts to reintroduce Przewalski horses to the wild in their former range, although since 1980 Przewalski horses have been released into large enclosed reserves in Holland, England, France, Hungary and Uzbekistan where they are essentially free living. The two sites chosen for reintroduction were Tachyn Tal, part of the Gobi B Strictly Protected Area, in the south western part of Mongolia where Przewalski horses were last seen in the wild, and Hustai National Park (HNP), a smaller area north of the centre of Mongolia (Plate 1.4). Tachyn Tal was set up by the German Christian Oswald Foundation and the Mongolian government, and Hustai National Park (HNP) was set up in 1990 by the Dutch Foundation Reserves Przewalski Horse (FRPH) in association with the Mongolian Association for the Conservation of Nature and the Environment (MACNE). Both reintroduction centres brought horses to Mongolia for the first time in 1992. The first horses were released from acclimatisation enclosures at HNP in 1994 and at Tachyn Tal in 1997. In July 2000 there were 51 horses at Tachyn Tal, 25 of which were free ranging, with another seven due for release that year. At the same time in HNP there were more than 100 horses, about 80 of which were free ranging. Tachyn Tal is now run by the International Takhi Group, an organisation using the same people that originally set up the site, but in cooperation with Salzburg zoo and the EEP. There was criticism of

how this reintroduction was originally run as it failed to follow the IUCN guidelines (Zimmermann, 1998). HNP is now primarily run by the Mongolians with decreasing Dutch assistance, but with funding guaranteed for the next five years by the Dutch government.

HNP and Tachyn Tal had similar survival (66% and 67% respectively) and death rates (34% and 33% respectively) since the first horses were brought to Mongolia, but Tachyn Tal had a higher mortality of imported horses (38%) to 1997 (Zimmermann, 1998). The Mongolian environment is very harsh and animals die during the winter, or else in the spring when the horses are in poor condition. In addition, there have been mortalities at both sites caused by the tick borne blood disease babesiosis (piroplasmosis). In HNP 23% of all deaths have been due to this disease (Magash, 2000) and at Tachyn Tal a possible 41% (Walzer *et al.*, 2000). *Babesia equi* and *B. caballi* are both endemic to Mongolia and are passed on to horses by the tick *Dermacentor nutalli*. Unless treated 25% to 100% of cases are fatal (West, 1992). However, animals can acquire immunity as mortality depends on the general immune status of the animal, its age, and the virulence of the piroplasm (Ruegg *et al.*, 2002). Foals of immune mares can be infected during pregnancy, but also go through an inapparent infection due to the protection of maternal antibodies (Ruegg *et al.*, 2002). Thus the local domestic horses and Przewalski horses born in Mongolia do not appear affected by the disease. On the other hand, newly introduced animals with no immunity and that are stressed for reasons such as transport, social stress, or bad condition in the early spring are likely to be especially susceptible.

In HNP a second generation of wild-born horses are nearing dispersal age and the population appears to be self-sustaining needing minimal human intervention. No more horses are going to be imported to this population. Horses will continue to be brought to Tachyn Tal for acclimatisation and reintroduction for the foreseeable future, but as more foals are being produced each year the population is also growing naturally.

1.4 Home range and habitat use

1.4.1 Social organisation

In the Pliocene and Miocene the equids were the most abundant medium sized grazing animal in the grasslands of Asia, Africa and the Americas. Today the genus *Equus* contains three species of zebra, three species of ass and two species of horse (Waring (1983); Table 1.2). Three of the equid subspecies recorded during the 20th Century have become extinct in the wild and thirteen are threatened (Duncan, 1992b). Although the equid species are not structurally diverse, the social organisation is different across the species. Female (harem) defence and resource defence polygyny have both been observed in wild and feral equids. These were referred to as Type I and Type II respectively by Klingel (1975). Animals showing female (harem) defence polygyny normally live in stable non-territorial groups of one or more stallions with a group of mares and their offspring (e.g. plains zebra (*Equus quagga*), mountain zebra (*E. zebra*), Asiatic wild ass (*E. hemionus*), and the feral domestic horse (*E. caballus*)). Resource defence polygyny is seen in Grevy's zebra (*E. grevyi*) and the African wild ass (*E. africanus*) in both its wild and feral domestic forms, and has been recently described in the Asiatic wild ass in Israel (Saltz *et al.*; 2000). Some stallions of these species maintain territories which are only defended when an oestrus female is near, and within which they have exclusive breeding rights. The only stable social unit is that of a female and her offspring, although groups of males, females or mixed sexes do occur (Moehlman, 1998b; Rubenstein, 1981).

Jarman (1974) hypothesised that dietary selectivity, anti-predator behaviour and body size affected group size, and so social system, in species of African antelopes, and this was also supported by the analyses of Brashares *et al.* (2000). It is likely that similar factors affect equids and evolution of the two social systems have been attributed to habitat differences (Rubenstein, 1981; Rudman, 1998). In particular it is thought that animals in a mesic habitat are more likely to have a female defence polygyny organisation, as a relatively open environment with evenly distributed food and water resources will result in females living in groups, so males can attempt to monopolise them (Moehlman, 1998b). Animals living in arid environments with patchy resources will suffer less competition if they live in smaller groups and have a resource defence polygyny organisation (Moehlman, 1998b; Rudman, 1998). When the movements of females are predictable, but their grouping is temporary, males will

Table 1.2. Species and subspecies of the genus Equus extant in the 20th Century. Status and distribution are from the Action Plan for the Conservation of Wild Equids (Duncan, 1992).

Chromosome number (2n)	Subgenus	Species	Subspecies	Distribution	Status
66	*Equus* (Horses)	*przewalskii*	*E. przewalskii* (Przewalski horse)	Mongolia	Extinct in the wild (reintroduced)
64		*caballus*	Domestic horses	Worldwide	
62	*Asinus* (African wild asses)	*africanus*	*E. a. africanus* (Nubian wild ass)	Ethiopia, Somalia	Critically Endangered
			E. a. somalicus (Somali wild ass)	Ethiopia, Somalia	Critically Endangered
			Domestic donkeys	Worldwide	
56	*Hemionus* (Asian wild asses)	*hemionus*	*E. h. hemionus* (North Mongolian khulan)	Mongolia	Indeterminate (probably extinct)
			E. h. luteus (Gobi khulan)	Mongolia, China	Insufficiently known
			E. h. kulan (Kulan)	Turkmenistan, Kazakhstan	Endangered
			E. h. onager (Onager)	Iran, Israel	Critically Endangered
			E. h. khur (Indian wild ass)	India	Endangered
			E. h. hemippus (Syrian wild ass)		Extinct 1927
		kiang	*E. k. kiang* (Western kiang)	Nepal, India, China	Indeterminate
			E. k. holdereri (Eastern kiang)	China	Abundant
			E. k. polyodon (Southern kiang)	China, Sikkim	Indeterminate
46	*Dolichohippus* (Grevy's zebras)	*grevyi*	*E. g. grevyi* (Grevy's zebra)	Kenya, Ethiopia	Endangered
44	*Quagga* (Plains zebras)	*burchelli*	*E. b. boehmi* (Grant's zebra)	Western/central Africa	Abundant
			E. b. crawshayi (Crawshay's zebra)	Malawi, Mozambique, Zambia	Abundant
			E. b. zambeziensis (Upper Zambezi zebra)	Zaire, Angola, Zambia	Indeterminate
			E. b. chapmani (Chapman's zebra)	Mozambique	Endangered
			E. b. antiquorum (Damara zebra)	Namibia (N), South Africa	Abundant
			E. b. burchelli (Burchell's zebra)		Extinct 1930
32	*Hippotigris* (Mountain zebras)	*zebra*	*E. z. zebra* (Cape Mountain zebra)	South Africa	Endangered
			E. z. hartmannae (Hartmann's mountain zebra)	Namibia, Angola	Vulnerable

be more likely to hold a territory (Saltz *et al.*, 2000), because if a male controls access to limiting resources, such as a water source, he will then be more likely to gain access to females (Emlen & Oring, 1977). This appears to be borne out by research on feral asses (Moehlman, 1998; Moehlman *et al.*, 1998; Rudman, 1998; Woodward, 1979), and Asiatic wild asses (Saltz *et al.*, 2000). However, in other ungulates female defence polygyny has been observed in conjunction with resource defence (Emlen & Oring, 1977) and it is possible both may be occurring in instances of resource defence polygyny. Also despite the theory appearing to hold true for African wild asses, there is only one case of supposed territoriality in feral horses (Rubenstein, 1981), despite their occurrence in a very wide range of habitats spanning mesic to arid.

Whether resources or females are defended will be affected by their distribution in time and space, and the time and energy that the male can afford for defence of mating access (Clutton-Brock & Harvey, 1978). Asiatic wild asses in Mongolia were observed to have a harem defence polygyny even though they live in a very arid environment with patchy resources (Feh *et al.*, 1994). The case of territoriality in horses (Rubenstein, 1981) was at least partly due to the habitat and geographical features of the island on which it was observed, enabling a stallion to easily monopolise an area. A similar phenomenon was observed in Przewalski horses when they were kept on two pastures separated by a fence, but with access through a gate. A stallion was observed to restrict access through this gate and so in effect defend an area (Kolter *et al.*, 1999).

There is currently debate as to whether territoriality *per se* has been shown in equids (Linklater, 2000), and it is possible that records of it are due to ill-defined terms. Ultimately it is likely that equids have an adaptable social system that may depend on local factors and particular requirements of the species (Woodward, 1979). Reintroduced oryx (*Oryx leucoryx*) were observed to totally change their social structure after rainfall (Tear & Ables, 1999). As conditions deteriorated after rain, subordinate males were no longer tolerated within herds, as they had been after release, and groups became smaller. In addition territorial behaviour was observed. This plasticity makes them suitable for reintroduction, as they will be more likely to survive under different conditions (Tear & Ables, 1999). There was a relationship between range size and group size or forage biomass in three out of the five cases where it was examined in horses (Linklater, 2000), so it is likely the social structure together with environmental conditions will affect the range size of the animals.

Little is known about the social system of Przewalski horses in the wild. Early explorers observed groups of 50 to 100 animals and stallions were observed to drive groups of mares (Mohr, 1971), but it is not really possible to infer the social system from these anecdotes. For most of the last century Przewalski horses were sent to zoos in pairs to breed (Bouman & Bouman, 1994; Klimov & Orlov, 1982), and it is only relatively recently that they were placed in harem and bachelor groups on the assumption that this is most likely how they lived in the wild. It will therefore be interesting to see if reintroduced Przewalski horses maintain their current harem defence polygyny social system (c.f. Tear & Ables, 1999).

1.4.2 Home range

Burt (1943) defined the home range as the "area traversed by the individual in its normal activities of food gathering, mating and caring for young", whereas a territory is a protected or exclusive part of that home range that has a social significance (Leuthold, 1977). The size of a home range must be large enough to provide an adequate supply of resources, but ultimately its size will depend on factors such as environmental conditions, primary production, dispersion of resources, metabolic requirements, predation and social pressures (Geffen *et al.*, 1999). In general, larger species, or those that live in large groups, and that are herbivores will have larger home ranges than smaller, or non-herbivore animals (Clutton-Brock & Harvey, 1978). Knowledge of the home range of an animal is important in relation to its management as it will enable potential carrying capacities and, in the case of a herbivore, potential grazing pressure to be predicted.

There are published works on the home ranges of more than 21 populations of feral horses (Linklater, 2000). In almost all cases the harems lived in undefended non-exclusive home ranges to which they showed long term fidelity and in which there tended to be seasonal changes in range size or use (seen in all populations in which it was examined) (Linklater, 2000). Habitat quality (i. e. the dispersion and quality of resources) is likely to be a primary determinant of home range size (Leuthold, 1977). Strongly clumped, widely dispersed or unpredictable resources will cause larger home ranges to be found than in areas with predictable and evenly distributed food (Clutton-Brock & Harvey, 1978), and this may also affect the overlap of home ranges (Miller, 1983a). There is evidence of this in horses as those in the relatively lush habitat of southern England and the barrier islands of the eastern coast of the United States tend

to have relatively small ranges of between 2.5 km^2 and 11.4 km^2 (Gates, 1979; Rubenstein, 1981; Tyler, 1972; Zervanos & Keiper, 1979), whereas horses in the semi-arid regions of the mid-west of America had ranges between 3 km^2 and 303 km^2, depending on season (Berger, 1977, 1986; Feist & McCullough, 1976; Miller, 1983b). Within the New Forest, Tyler (1972) found that when resources such as grazing and resting areas, shelter and water were close together, the home range was smaller than when they were dispersed. The horses probably alter their range use to make the best use of available vegetation, as seen in other animals. Before rainfall the oryx in Oman used a large area, but following rain tended to decrease their range to just use the areas where the vegetation had recovered from drought (Corp *et al.*, 1998).

When animals are newly reintroduced they will have very little competition from conspecifics so theoretically could settle in a home range that covers the best resources. In practice it is likely that an animal will initially settle near its acclimatisation site (e.g. the black rhinoceros, *Diceros bicornis* (Stanley Price, 1991)), although when released oryx encountered signs of animals released before them they dispersed to previously unoccupied areas (Stanley Price, 1991).

Some populations of horses have been reported to move as a herd, i.e. the whole population forms a cohesive group. However although the harems follow similar movement patterns within overlapping home ranges they remain spatially separate (Miller, 1983b; Miller & Deniston, 1979). As almost all horse populations show extensive range overlap (Linklater, 2000), it is possible that they need to come into contact with other harems for protection from predation, or to encourage dispersal of animals to other harems to reduce inbreeding, or even to reduce the effects of biting flies (Duncan, 1992a). Therefore after release from acclimatisation enclosures it might be necessary for animals to be aware that others are in the area. This will also prevent young animals from dispersing too far from a protected area because they can join bachelor groups or other harems.

Forage, water and shelter may be the most important factors affecting home range size, but factors such as the weather and presence of insects may also have an effect on the use of different areas. Caribou (*Rangifer tarandus*) are affected by biting flies at certain times of the year and this affects their grouping and choice of habitat (Bergerud, 1974). Horses have been shown to select ridge tops, snow patches, or open ground in an attempt to reduce the number of flies around them (Duncan & Cowtan, 1980; Keiper & Berger, 1982; Rubenstein & Hohmann, 1989; Rutberg, 1987). When

animals are avoiding flies, they have less time to forage, thus biting flies become a cost greater than the blood that they may consume. There are differing patterns of range use over the seasons in different populations. Berger (1977) and Linklater *et al.* (2000) found that home range sizes increased in the winter in the Grand Canyon and the North Island of New Zealand respectively, whereas Zervanos and Keiper (1979) on Assateague Island, and on Exmoor, Gates (1979) reported smaller home ranges in the winter. Ruminant herbivores in North America showed a reduction in home range in the winter, because although they can find sufficient food, they are limited by the constraints of processing it (Harestad & Bunnell, 1979). Cattle in the cold desert of Utah altered their behaviour in the winter to minimise energy expenditure during periods of extreme cold (Malechek & Smith, 1976). A similar reaction would be expected in horses, and in the Red Desert they were observed to alter their habitat use to spend more time near ridges where they could shelter from the wind in winter (Miller, 1986). A seasonal change in social structure has also been reported. Geffen *et al.* (1999) found that female mountain gazelles (*Gazella gazella gazella*) aggregated in larger groups in the winter, and Gates (1979) found a similar tendency in horses on Exmoor. Conversely Keiper (1976), Kimura (1998) and Rubenstein (1981) found the distance between horses to be greatest in winter, as they clump together during the summer to avoid the effects of flies, and Kaseda (1983a) noted a decrease in group size in the winter and related this to the sparseness of vegetation in this season.

1.4.3 Time budgets

Well defined daily patterns of behaviour have been observed in many species, but the basic trends observed in ungulates (activity in the morning and late afternoon and a resting period through the middle of the day) will vary from day to day and with the seasons (Leuthold, 1977). The time budgets of horses have been quite well studied, with both managed and feral domestic horses being examined (e.g. Berger (1986); Carson & Wood-Gush (1983); Duncan (1979); Feist & McCullough (1976); Keiper *et al.* (1980)). Przewalski horses have been observed in captivity (Boyd, 1988b; Boyd *et al.*, 1988; Boyd & Houpt, 1994), but there has been only one study of Przewalski horses in the wild which covered just a short period immediately before and after release (Boyd, 1998).

Horses spend more than 90% of each 24 hour period in either resting or foraging activities (Berger, 1986). Resting frequently occurs while standing and this has been

shown to be the posture of minimal energy demand on horses due to a 'stay apparatus' of the limbs enabling a leg to be locked in place (Waring, 1983). Most studies have shown this activity to occur during the middle of the day, and to be more common in the summer than winter, as a result of harassment by insects and for thermoregulation (Berger *et al.*, 1999; Kaseda, 1983b; Keiper *et al.*, 1980; Tyler, 1972). Lateral recumbency is needed for paradoxical sleep and is observed most between 0000h and 0400h (Boyd *et al.*, 1988), although it can occur during the day (Waring, 1983).

The amount of time spent feeding is likely to depend on the temperature and food density (Caraco, 1979). In cold weather energy requirements will be higher, and food density will affect the amount of time spent foraging. In horses, feeding has been observed to take up between 46% (Boyd *et al.*, 1988) and 75% (Salter & Hudson, 1979) of the day. It typically occurs in bouts in the early morning around dawn, and then again in the late afternoon or evening (Boyd *et al.*, 1988; Keiper & Keenan, 1980; Tyler, 1972). The time of day and actual time spent feeding depends on the season (Berger, 1977; Mayes & Duncan, 1986) and the management regime imposed on the animal (Waring, 1983). Boyd (1988) found a difference in the time budgets of Przewalski horses in different types of enclosure, with horses in small yards spending less time standing and more time feeding than those in a large enclosure.

Most studies found that horses graze more in the winter than the summer, probably to make up their nutritional needs from poorer vegetation (Berger, 1977, 1986; Duncan, 1985; Keiper *et al.*, 1980; Tyler, 1972; Zervanos & Keiper, 1979). However, some studies found that horses graze more in the summer than the winter (Kaseda, 1983b; Mayes & Duncan, 1986) with energy conservation being given as a possible explanation. Malechek and Smith (1976) found that grazing was the most costly behaviour energetically for cattle, yet they grazed more in the winter than the summer, possibly to keep warm, as well as in response to an increased 'appetite drive' due to cold weather. However on very cold days the cows spent less time grazing to conserve energy.

The remainder of a horse's time budget (usually about 10%) is taken up with other maintenance activities such as drinking, moving, and coat care, with some time also devoted to social interactions.

1.4.4 Vegetation use

Animals are believed to forage in a way that will maximise their energy intake under a particular set of circumstances (Krebs & Davies, 1993). Herbivores generally live in an environment that is abundant with potential, but low quality, food, so their biggest constraint is the time required to eat and process enough bulk to meet their nutritive requirements (Owen-Smith & Novellie, 1982). Therefore an optimal foraging strategy for a generalist herbivore should be to secure the best mix of nutrients within a fixed total intake of food (Owen-Smith & Novellie, 1982). In tests of stabled horses it was found that although they showed a definite preference for certain foods, their intake was not depressed when they were given an unpalatable food (Hawkes *et al.*, 1985). Owen-Smith and Novellie (1982) developed an optimal foraging strategy model for the greater kudu (*Tragelaphus strepsiceros*). Their assumptions dealt with the availability of nutrients to an animal, and that, "a 'clever ungulate', defined as a short-term maximiser for nutrient intake alone, should select a diet that maximises the intake rate of the most limiting nutrient during foraging periods". The kudus followed the model and were both selective and responsive in their food choice. However a slight deviation from the model was that they selected plants for their energy content more than their crude protein. Cattle were shown to be able to perceive variations in the quality and quantity of different hays in a test, and chose them as the optimal foraging strategy for maximum energy gain would predict (Ginane *et al.*, 2002).

Brashares *et al.* (2000) found that dietary selectivity correlated negatively with body mass and group size. Although this was applied to African antelopes it is probable that the same principles will hold true for horses on open grasslands and so they would be expected to feed unselectively on grasses, and possibly browse. Individual foraging efficiency of a large ungulate will increase with group size (to a certain limit) as they will not need to be so vigilant in large groups (Berger *et al.*, 1983).

Ruminants, particularly bovids, are thought to have had evolutionary success because of their highly efficient digestive system (Duncan, 1992a). Horses digest food in a caecum and although they are not so efficient at completely digesting food, they can assimilate more nutrients per unit weight and per day than bovids across the range of forage quality (Duncan, 1992a). Thus they do better on low quality pasture. It was observed that in winter, when there is less crude protein available, cattle selected a higher quality diet than horses, which appeared to be on a sub-maintenance nutritional

plane in this season (Krysl *et al.*, 1984b). Therefore they can survive by extracting nutrients from poor quality forage.

Recent research has been aimed at examining how horses can be used to manage nature reserves (Duncan, 1992a). In the 1980s a lot of research was carried out on the diet and impact on the vegetation of feral horses in the American west, as their large and fast growing populations may have an impact on both the native wildlife and cattle. Overgrazing is a real threat in semi-arid grasslands and can lead to a range dominated by unpalatable shrubs and forbs (Fernandez-Gimenez & Allen-Diaz, 1999; Smith, 1986). Fifty-nine per cent to 75% of the horses diet was similar to cattle in Colorado, but only 11% overlapped with the less diverse diet of mule deer (Hubbard & Hansen, 1976). In Wyoming the horses had a greater dietary overlap with cattle in winter (Krysl *et al.*, 1984a), but it is likely that the biggest cause of competition between the species will be the effect of trampling at water sources (Plumb *et al.*, 1984). This degrades the vegetation as well as affecting the water supply. Overgrazing occurred in a radius of up to 1.5 km around water holes in the Kruger National Park (Van der Schijff (1959) (in Penzhorn (1982)).

Roe deer (*Capreolus capreolus*) were observed to utilise the minimum area possible to sustain their energy requirements (Tufto *et al.*, 1996), and in general animals need to maximise their energy intake while minimising its expenditure (Berger *et al.*, 1983). Horses have been shown to preferentially use areas with the greatest concentration of high quality food, and will maximise their intake in these areas in any season (Duncan, 1983), whereas this was not observed in cattle (Putman *et al.*, 1987). An empirical habitat model showed that 73% of the variance of moose (*Alces alces*) density in a park in Canada was explained by habitat characteristics (Puttock *et al.*, 1996), and there is evidence that horses select their habitat on the basis of forage availability (Duncan, 1983; Salter & Hudson, 1978). This was the primary determinant of habitat utilisation in all seasons (Putman *et al.*, 1987; Salter & Hudson, 1979).

The quantity and quality of vegetation affects its value for a herbivore and both of these are likely to change with season (Duncan, 1992a). Seasonal change of diet in horses has been shown by several authors in America (Hansen, 1976; Krysl *et al.*, 1984b; Miller, 1983b) and England (Putman *et al.*, 1987). In addition to plant communities, shelter and surface water will affect the seasonal distribution of horses (Miller, 1983a). The bite rate of horses correlates negatively with the standing crop of

vegetation, so is therefore relatively low in summer, but needs to be higher in winter to enable sufficient bulk to be ingested (Putman, 1986).

Knowledge of the home ranges and habitat use of a population of animals will enable predictions to be made about their future spatial and temporal movements, and so is invaluable for the management of wild or reintroduced animals.

1.5 Social behaviour

1.5.1 Agonistic behaviour

Analysis of dominance hierarchies can enable a greater understanding of the social structure of animals, and allow hypotheses to be made about the benefits of dominance and its effect on sexual selection and the fitness of animals at different levels of the hierarchy. Dominance is implied from agonistic interactions between two individuals; the winner is said to have a dominant status and the loser is subordinate. When examined in a group of animals these positions can be used to form a rank hierarchy (Drews, 1993).

The effect of dominance rank on reproductive success has been hypothesised for both sexes. When maternal investment can influence the reproductive success of offspring, more should be invested in the sex with the higher variance in reproductive success (Trivers & Willard, 1973). For instance, in red deer (*Cervus elaphus*), as in many polygamous and sexually dimorphic ungulates, males have the higher variance in reproductive success, and dominant mothers tend to produce more sons (Clutton-Brock *et al.*, 1986). Dominant females tend to be in good condition (Clutton-Brock *et al.*, 1984) and are able to devote more resources to producing higher quality males, which in turn are more likely to be able to become dominant and have a higher lifetime reproductive success. A lower quality, subordinate, female will best enhance her reproductive success by producing daughters, as their breeding success will be less affected by their mothers rank (Clutton-Brock *et al.*, 1986). There is a correlation between the rank of a mother and her offspring in rhesus macaques (*Macaca mulatta*), which also positively affects their reproductive success (Smith & Smith, 1988). Trivers and Willard's (1973) hypothesis has implications for the composition of a reintroduced group of animals, as the age structure, and so dominance rank, of females may not reflect that in a wild population. This may lead to a skewed operational sex

ratio in the first years following release, thus slowing the growth of the population (Komers & Curman, 2000), as observed in a reintroduced Asiatic wild ass population (Saltz & Rubenstein, 1995).

There are costs and benefits to the animals in encounters which may affect or reflect their dominance status. To a certain extent, the escalation of a conflict will depend on the motivational state of the subjects. Paired feeding tests used to find the dominance order in a group of horses were not very reliable because of inter-individual variations (Ellard & Crowell-Davis, 1989), and this variation also affected the food choice of cattle (Ginane *et al.*, 2002). However in general the outcome is likely to follow an evolutionary stable strategy as predicted by game theory (Krebs & Davies, 1993). When water was a limiting resource for feral horses in North Carolina, it was found that the stallion of the harem occupying the water source at any particular moment won most contests against stallions of harems approaching the water, regardless of their respective ranks (Franke Stevens, 1988). This follows the evolutionary stable strategy that the resident will escalate a contest until the opponent retreats, since he will potentially suffer greater costs by losing access to the resource. On the other hand, the intruder will display, and retreat if the opponent escalates, because he will suffer greater costs by being injured than by waiting or finding an unoccupied resource (Franke Stevens, 1988).

The benefits of being dominant include better access to limited resources. Dominant reindeer (*Rangifer tarandus*) had better access to prime food resources, such as patches cleared of snow, which enabled better winter survivorship (Espmark, 1974), and dominant harems of horses had better access to water sources (Miller & Deniston, 1979) and possibly better forage areas. However dominance also has costs. It was found that the offspring of dominant reindeer had the greatest infestation of parasites (Halvorsen, 1986), possibly as they used the best food areas where there will be the greatest concentration of animals, and dung (Rubenstein & Hohmann, 1989). On the other hand, the pathenogenicity of the parasites will be reduced as dominant animals will be in better condition, and so able to tolerate a higher parasite load, than subordinates, but only up to a certain point. After that point they will lose condition and so will suffer a reduction in their competitive fitness and will not be as likely to reproduce with other dominant animals, thus reducing inbreeding (Halvorsen, 1986). Dominant animals also run a greater risk of injury in contests. Fights between evenly matched zebras (*Equus burchelli*) and onagers (*E. hemionus*) carried greater risks of

injury, and an injured male was less likely to maintain a harem (Berger, 1981). In addition, dominant animals have been shown to have higher levels of stress hormones (Creel *et al.*, 1996) which could lead to a shorter life span (Weeks *et al.*, 2000).

The dominance rank of animals is correlated with several factors such as age, weight, length of time in a group and matriline or mothers rank. However, the weighting of these factors may be altered by circumstances and the dominance of an individual could simply be related to its level of aggression (Tyler, 1972). In most studies of horses, rank has been correlated with age, weight and height (Ellard & Crowell-Davis, 1989; Keiper & Receveur, 1992; Keiper, 1988; Keiper & Sambraus, 1986; Tyler, 1972; Wells & von Goldschmidt-Rothschild, 1979). Larger harems as a whole tend to be dominant over smaller ones (Miller & Deniston, 1979), because the stallions of large harems are usually dominant over the stallions of smaller harems (Berger, 1977). Rutberg and Greenberg (1990) observed more aggression per head in larger harems, which was independent of the distance between individuals. Higher ranking mothers of domestic horses produced daughters that ranked higher as foals (Weeks *et al.*, 2000), and then were more dominant in their own right in another harem (Houpt *et al.*, 1978). The mother's rank was also correlated with her reproductive success (Feh, 1990).

In rhesus macaques, related adults were closer in rank position than unrelated individuals. Disparity of rank between individuals affected many aspects of their social behaviour independently of kinship and so was a central feature of their social organisation (de Waal, 1991). A similar effect is likely in horses: thus dominance rank will affect all activities in their daily lives.

1.5.2 Associative behaviour

Social behaviour other than aggression is quite rare in horses (Wells & von Goldschmidt-Rothschild, 1979), but is expressed as allogrooming, also referred to as mutual grooming, or simply by horses standing in close proximity. Allogrooming has been reported to have several functions, but the proximate reason is the removal of loose hair and endoparasites from areas of the body that the animal cannot reach by itself (Dunbar, 1991; Feist, 1971; Schino *et al.*, 1988). Mutual grooming is described by its name – when two animals stand, normally reverse parallel, and nuzzle or pull at each others coats with their teeth. In the literature there are conflicting reports whether this most frequently occurs between kin (Houpt & Boyd, 1994; Wells & von

Goldschmidt-Rothschild, 1979), animals of similar age and rank (Keiper & Receveur, 1992; Keiper, 1988), or if there is no influence of rank or kin (Clutton-Brock *et al.*, 1976; Mooring & Hart, 1995). In primates there was also a correlation between group size and frequency of grooming (Dunbar, 1991).

Mutual grooming carries costs as well as benefits, such as tooth wear, and loss of water in saliva used for grooming, but most importantly, in impala (*Aepyceros melampus*) it has been shown to reduce the vigilance of the participants (Mooring & Hart, 1995). However most grooming will take place to remove ticks, and it is likely that the cost of loss of blood to ticks is a greater cost than the risk of predation. As well as causing disease, ticks can have a considerable effect on an animal, a moderate tick load on calves resulted in 10 kg to 44 kg reductions in weight gain per year (Mooring *et al.*, 2000). Smaller animals need to groom more than large ones. They will incur higher costs per tick because of their body mass to surface area ratio, and across species there is a negative correlation between mass and grooming bouts per hour (Mooring *et al.*, 2000). Within species, a similar relationship would be expected between smaller, young animals and larger adults, and more frequent mutual grooming has been recorded among foals than their mothers (Wells & von Goldschmidt-Rothschild, 1979), although this hasn't been shown in all populations (Keiper & Receveur, 1992). Allogrooming in primates has been found to focus primarily on areas of the body that the animal could not reach by self grooming, showing the important utilitarian function of this activity (Barton, 1985).

Mutual grooming appears also to have a social component, and in horses it has been widely thought to strengthen bonds between animals or family members (Crowell-Davis *et al.*, 1986; Feist & McCullough, 1976), and was observed to be more common in the summer, when horses stay closer together (Kimura, 1998). It has been reported to have a function for appeasement, either to ameliorate aggression (Feh & de Mazieres, 1993; Feist & McCullough, 1976), or to reduce weaning conflict (Keiper, 1988; Penzhorn, 1984), when it is the younger (or subordinate) animal than initiates the session. Mutual grooming has been recorded to reduce the heart rate of participating horses, and thus would act to reduce social tension (Feh & de Mazieres, 1993). Similarly, among Java monkeys (*Macaca fascicularis*) allogrooming reduced the frequency of male displacement activities, which were taken as a sign of tension (Schino *et al.*, 1988). The important social function of mutual grooming was also shown in a study where more mutual grooming was seen in a new group of horses in

an area with few parasites, than in an established group in an area with few parasites (Feh & Carton de Graumont, 1995). Therefore it is likely that although mutual grooming evolved as a purely hygienic function it has developed a more social significance (Dunbar, 1991).

1.5.3 Marking behaviour

Scent marking of some description is seen in most animals and although it has been well documented its function is still little understood (Brashares & Arcese, 1999). There have been several hypotheses, such as marking a territory to deter intruders, to provide them with information on the status of the territory owner, or to orient the owner within its territory (Gosling, 1982). There are three main occurrences of scent marking: it occurs commonly, but not exclusively, at socially important or well used areas; it is mostly carried out by high ranking animals; and it often occurs during agonistic encounters (Leuthold, 1977). One hypothesis for the function of scent marking is that it can be used as a means of assessment to the benefit of both the owner of a territory and an intruder (Gosling, 1982). If the marks within a territory match that of an animal encountered by an intruder it is likely that this animal is the owner. As animals who hold territories are likely to be high quality, and probably have more to gain in holding the territory than the intruder does in taking it over, it will pay the owner to escalate a conflict and the intruder to retreat. In this way marking can help reduce the costs of territory defence, and reduce the risk of injury to an intruder (Gosling, 1982). This hypothesis will hold true for animals that use female defence polygyny, as males marking female excrement are declaring that they are her consort.

Various excretions are used in scent marking. Many species of African bovid mark twigs and grass stems with excretions from the antorbital gland, and other species spray urine on themselves which they then rub on to females or the vegetation (Leuthold, 1977). In the Perssiodactyla, tapirs and rhinos squirt urine at certain places, and also wallow and rub in mud that contains their faeces (Moehlman, 1985). All Perissodactyls are observed to flehmen and use stud piles (Moehlman, 1985). Faecal material is good for scent marking as it is relatively persistent in the environment, it has a minimal energetic cost to the signaller, and it forms a substrate for glandular secretions (Brashares & Arcese, 1999). Dung piles can get quite large and so also provide a visual signpost, especially if they are placed in open areas (Salter & Hudson,

1982). However it is still not known whether the odoriferous substances are contained in the faeces themselves, or if they originate from special glands (Leuthold, 1977).

Marking of female eliminations and formation of stud piles has been observed in most populations of equids. It appears to be related to dominance since marking is almost entirely carried out by the stallion, and the most dominant stallion of a group will mark last on a pile, thus providing an immediate visual and olfactory impact in terms of dominance relationships (Feist & McCullough, 1976; Miller, 1981). Marking was rarely observed in juvenile horses (Feist & McCullough, 1976), and was not observed in rhinos that did not hold a territory (Rachlow *et al.*, 1999). Klingel (1972) thought that marking behaviour only had a purpose in territorial equids (to delineate the territory and orientate the owner), and in non-territorial species it was purely a vestigial pattern inherited from their territorial ancestors. However it has been shown to have an important function in social interactions and gives information on the associations and sexual state of the marker (Feist & McCullough, 1976). Rubenstein and Hack (1992) also found the importance of marking and vocalisations in enabling horses to determine the fighting ability and/or identity of a contestant. They found that dung of unfamiliar stallions was examined for almost twice as long as that from familiar, thus stallions were able to discriminate among known individuals. However they showed no difference in their response to the dung of dominant and subordinate males, but had a strong response to their respective vocalisations. Stud piles, and other forms of marking, could almost be thought of as analagous to writing, since they provide chemical information which will persist through time (Feist & McCullough, 1976). Marking must be important in the social interactions of equids, as in many species, as the stimuli almost always provoke a strong a ritualised response (Turner *et al.*, 1981).

1.5.4 Vigilance behaviour

Many authors have reported that individual vigilance is reduced with increasing group size (reviewed in Elgar, 1989 and Quenette, 1990), and this is known as the many eyes hypothesis. As well as a reduction in individual vigilance, living in a group can help an animal avoid predation by the dilution effect – if an animal is in a large group then the chances of being picked out by a predator are that much smaller. Vigilance decreases with increase in group size for three measures: total herd size, number of conspecifics, and the number of heterospecifics in the herd (Scheel, 1993). Predators

are more likely to take the least vigilant animal in a group (Fitzgibbon, 1988) and so it benefits all animals to be equally vigilant. An animal is also at an advantage if it is vigilant because, as the first animal to spot a predator it is most likely to be able to avoid capture (Lima, 1994). However, an animal cannot normally forage and be vigilant at the same time so vigilance bears costs, although these costs can be ameliorated (Underwood, 1982).

The level of vigilance of an animal will be affected by the density and type of food, body mass, competition between individuals, habitat, proximity to refuge, reproductive condition, sex, time of day, temperature, and potential predation pressure (Berger & Cunningham, 1988; Elgar, 1989). The amount of foraging time spent scanning scales negatively with body mass (Illius & Fitzgibbon, 1994), so larger animals spend less time scanning than small. Smaller animals are more susceptible to predation, but will also incur fewer costs by spending more time scanning because they tend to live in a more closed habitat where they can feed more selectively in an area of higher plant density (Illius & Fitzgibbon, 1994). Larger animals incur higher costs; vigilance produces a time constraint on feeding, although scanning can also help animals locate food patches (Underwood, 1982). However, animals in large groups might then be forced to compete for these patches. Berger *et al.* (1983) found that pronghorns (*Antilocapra americana*) remained in large groups in areas of high disturbance even though they were foraging less profitably. Habitat was shown to affect the vigilance behaviour of ground squirrels (*Spermophilus townsedii*); they were able to be less vigilant in open areas than closed patches (Sharpe & Van Horne, 1998). Habitat will also affect the distance an animal has to flee to a refuge. Dall's sheep (*Ovis dalli dalli*) became less vigilant as group size increased, but more vigilant as they moved farther from cliffs, their refuge (Frid, 1997). These two factors worked interactively, so that the sheep were more vigilant farther from cliffs regardless of group size, and vice versa.

Anti-predator behaviour is observed in African ungulates which simply consists of avoiding thickets where predators are likely to lie in wait, drinking during the day (as most predators hunt more at night (Schaller, 1976)), and walking in single file so as to have a clear escape route (Leuthold, 1977). Impala (*Aeopyceros melampus*) that were rearmost when moving in a line were thought to be least at risk, but were also the most vigilant, suggesting that vigilance also plays an important part in group cohesion (Underwood, 1982). Wildebeest (*Connochaetes gnou*) and zebra were observed to

scan more when lions (*Felis leo*) were most active (Scheel, 1993), and can adapt their flight distance and defensive behaviour to each predator (Schaller, 1976). When scanning, animals scan the other members of the group, as well as the environment (Lima, 1995), and alert postures and alarms have been shown to be the most allelomimetic behaviour in gregarious antelope (Jarman, 1974), drawing the attention of the whole group to a potential threat.

There is a danger that animals captive-bred for reintroduction will have lost recognition of potential predators and so will suffer heavy losses after release (Price, 1999). In areas where wolves have been extirpated by man, moose (*Alces alces*) no longer respond to the alarm call of a raven as a potential warning to the presence of wolves (*Canis lupus*) (Berger, 1999). However animals can learn anti-predator behaviour. High rates of mortality from predation were observed among captive-reared bighorn sheep (*Ovis canadensis*) in the first six months after release; however these rates declined as the surviving animals entered their second year in the wild (Osterman *et al.*, 2001). Experiments preparing captive bred rufous hare-wallabys (*Lagorchestes hirsutus*) for release (McLean *et al.*, 1996), and some involving laboratory bred deermice (*Peromyscus* sp.) (Hirsch & Bolles, 1980), have shown that these animals do retain responses to predators, while Griffin *et al.* (2000) found that pre-release anti-predator training can enhance existing anti-predator behaviour. In the case of the hare-wallabys, the predators that they will face on release were not present when they became extinct in the wild, but it is possible that they have a general response to a large predator, or simply an unfamiliar animal. Deermice were shown to only have a reaction to predators that were found in their native habitat, showing an added importance of reintroducing an animal to its historical range.

1.6 Effects of flies

Parasites have a strong effect on the behaviour of many animals (Mooring & Hart, 1992). While animals are being attacked by flies they do not feed, and often move to areas where the quality of potential forage is lower (Keiper & Berger, 1982). Flies, particularly members of the Muscidae and Calliphoridae, can affect animals by transmitting endoparasites and many diseases to animals, including anthrax and several types of encephalitis (Askew, 1971). Flies from these families cause great annoyance to animals by feeding from secretions around their faces, but their maggots

may also infest wounds, often enlarging the injury and causing infection (Evans, 1984). The families of flies that have the greatest physical affect on horses are the Tabanidae and Gasterophilidae. Tabanidae can take a considerable amount of blood: 300 to 500 ml in a day when in large abundance (Tashiro & Schwardt, 1953), and are the cause of fly avoidance behaviour in most horse populations (Duncan & Cowtan, 1980; Keiper & Berger, 1982). Gasterophilidae lay their eggs on the fur of animals, then when licked off the larvae hatch into the mouth of the animal and migrate through the epidermis to attach themselves as parasites in the intestinal tract (Oldroyd, 1964). These flies cause great distress to grazing animals, even though the adult flies do not directly cause pain, and the animals may be so stressed they stampede, or can prevent their young from nursing (West, 1992).

Flies appear to be responsible for a change in habitat use and social grouping in several species. When fly abundance is high feral horses, reindeer and red deer have been observed to use areas exposed to the wind, like bare patches of ground or ridges, to rest (Bergerud, 1974; Clutton-Brock *et al.*, 1982; Duncan & Cowtan, 1980; Zervanos & Keiper, 1979), and some African monkey species and reindeer change their social structure by forming groups (Bergerud, 1974; Rubenstein & Hohmann, 1989). The same theories of group formation that apply to protection from predation, the encounter-dilution and selfish herd effects, can also be applied to protection from attack by parasites (Mooring & Hart, 1992). Animals in larger groups have fewer flies per individual than those in smaller groups (Duncan & Vigne, 1979), and dominant animals tend to be situated more toward the centre of the group (Mooring & Hart, 1992). The tendency for animals to group to ameliorate the effects of flies is limited by larger groups being more exposed to infection by endoparasites (Rubenstein & Hohmann, 1989). Thus although the behaviour of the animals may be dictated by the ectoparasites, by entailing higher costs endoparasites will play a stronger role in controlling the social structure of a population (Rubenstein & Hohmann, 1989).

1.7 Aims

The overall aim of this study is to examine the behavioural ecology of Przewalski horses released into the wild at Hustai National Park, Mongolia, with particular reference to how they utilise their habitat. The results of this study should provide information for the management of Przewalski horse populations, and aid future reintroductions.

Specific aims are:

1) To examine the home ranges of harems to find whether there are any differences in size and resource abundance according to location, group size, length of time released, environmental factors and composition of the habitat, including vegetation use.
2) To examine the horses' use of vegetation with respect to the season, and the bite rate on different vegetation types and by different ages and sexes.
3) To analyse effects of time and environmental factors on the time budget of the horses, as well as any differences according to location, group size, and length of time released. The synchronicity of behaviour of the harems will be examined.
4) To examine the frequency of agonistic behaviour in relation to age and sex, group size, and the behavioural elements used. Agonistic behaviour will also be used to determine dominance hierarchies for each harem. Effects of age, tenure in the harem and frequency of aggression will be examined.
5) To examine the frequency of associative behaviour and its constitutive behavioural elements in relation to time of year, relatedness, dominance rank, age, tenure in the harem and frequency of aggression.
6) To analyse differences in stimulus and terrain subjected to marking behaviour, and behaviours used to mark. Possible relationships between home range boundary and stud pile placement will be examined.
7) To examine the frequency of vigilance with respect to different levels of vigilance, time, stimulus, group size, length of time released, age and sex, tenure in the harem and frequency of aggression.
8) To examine the abundance of flies in different areas used by the horses and the diversity of families across the site. Effects of flies on the Przewalski horses will be analysed by examining their comfort behaviour under different environmental conditions.

Chapter Two

Methods

Chapter 2. Methods

2.1 Study site

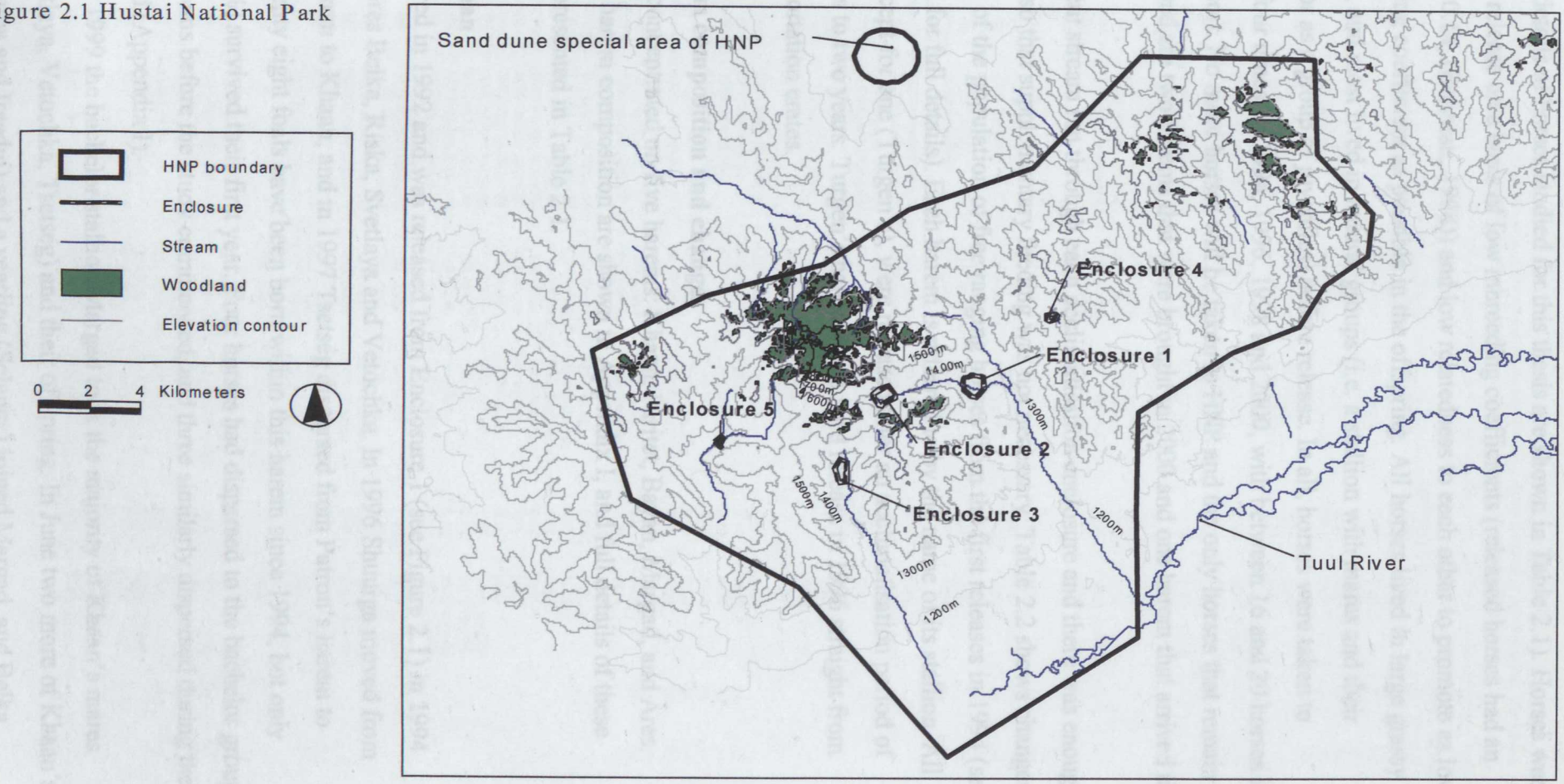
All fieldwork was carried out at Hustai National Park (HNP), Mongolia between June 1998 and July 2000. HNP is situated about 150km south west of Ulaan Baatar, the capital city of Mongolia (Plate 1.4). It covers 570 km^2 along a south western spur of the Khentei range of mountains (around the geographical coordinates: 47° 41' N, 105° 54' E). The park borders the Tuul river, and has an altitude of between 1100 m and 1842 m. The climate is continental with a mean annual temperature of +0.2°C and a yearly precipitation of 270 mm, most of which falls as rain in the summer (Wallis de Vries *et al.*, 1996). During the study period, horses were observed in temperatures of between –14°C and +34°C. HNP has a mountain forest steppe habitat which consists of steppe, meadow, grassland, shrub and woodland communities (Wallis de Vries *et al.*, 1996). Asian white birch (*Betula platyphylla*) forest covers 5% of the park on the northern slopes. Water flows down most of the major valleys as streams, which are permafrost fed and covered by gravel at places along their length (Figure 2.1). Several species of large ungulate are found in the area, including red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), the internationally threatened Argali sheep (*Ovis ammon*), and Mongolian gazelle (*Gazella guterosa*). There are several species of carnivore, such as mustelid and fox species, lynx (*Felis lynx*), Pallas' cat (*Felis manul*) and wolves (*Canis lupus*). The bobak marmot (*Marmota bobak*) is common.

The area was made a reserve in 1993 in preparation for the release of Przewalski horses (Bouman, 1998) and designated a National Park in 1999. Before the site was protected it was used by nomads to graze their livestock and these people still live around the edge of the park.

2.2 Study animals

Most of the horses released came from reserves owned and run by the Foundation Reserves Przewalski Horse (FRPH) in Holland, but some horses also came from Askania Nova in the Ukraine, and zoos in Germany and England (the background and

Figure 2.1 Hustai National Park



stud book details of horses studied for this thesis are shown in Table 2.1). Horses were chosen for release on a basis of low inbreeding coefficients (released horses had an average of 0.14, (Bouman, 1998)) and low relatedness to each other to promote as low an inbreeding coefficient as possible in the offspring. All horses lived in large grassy enclosures, and most lived in natural groups (i.e. a stallion with mares and their offspring, or as a group of juveniles) before release. In all, horses were taken to Mongolia four times, in 1994, 1996, 1998 and 2000, with between 16 and 20 horses in each transport. No more horses will be taken to HNP and the only horses that remain to be released are two harems that were brought in 2000 and one harem that arrived in 1998.

A permanent stream ran through each acclimatisation enclosure and there was enough vegetation so that supplementary feeding was not necessary. Table 2.2 shows changes and growth of the population of free ranging horses from the first releases in 1994 (see Appendix I for full details). Each harem is referred to by the name of its stallion. All harems, except for one (Turgen's), were released after an acclimatisation period of four months to two years. Turgen's harem had a hard release in 1996 straight from their transportation crates.

2.2.1 Harem composition and changes

This study concentrated on five harems: Khaan, Paritet, Bayan, Margad, and Ares. Changes in harem composition are shown in Appendix I, and full details of these horses are presented in Table 2.1.

2.2.1.1 Khaan

Khaan arrived in 1992 and was released from Enclosure 1 (see Figure 2.1) in 1994 with the mares Belka, Riska, Svetlaya and Vetochka. In 1996 Shuurga moved from Paritet's harem to Khaan, and in 1997 Tsetseg dispersed from Patron's harem to Khaan. Twenty eight foals have been born within this harem since 1994, but only fifteen (54%) survived their first year. Four horses had dispersed to the bachelor group or other harems before the study commenced, and three similarly dispersed during the study period (Appendix I).

In January 1999 the bachelor stallion Margad took the majority of Khaan's mares (Riska, Svetlaya, Vetochka, Tsetseg) and their offspring. In June two more of Khaan's mares (Shuurga and Ireedui) and a yearling (Selenge) joined Margad, and Belka

Table 2.1. Studbook details of horses studied at HNP. Horses in other harems and those born and dispersed before the study commenced are not included. Harem indicates harems that the horse has spent time in and where they were in July 00. Pa=Paritet, Bo=Bohemian, Kh=Khaan, Ba=Bayan. Tu=Turgen, Ma=Margad, Mang=Mangir, Mark=Mark, Manl=Manlai, Bach=bacehlor group and Ar=Ares harem.

Name	Sex	Harem	Stud book reference	Father	Mother	Inbreeding coefficient (F)	Birth	Death	Year of arrival	Year of release
Paritet	m	Pa	1846 Askania 180	970 Paris	525 Golubka	0.17	1989		92	95
Ayunga	f	Bo>Pa	1459 Lelystad 8	915 Apoll	1083 Lory	0.16	1986		98	98
Naidvar	f	Pa>Kh>Pa	2183 Ooij 12	1278 Vagur	1314 Nyam	0.09	1991		94	95
Boroo	f	Pa	2219 Lelystad 27	915 Apoll	1001 Nora	0.14	1991		94	95
Buyana	f	Pa	2189 Lelystad 25	915 Apoll	769 Laura	0.13	1991		94	95
Tengis	f	Pa	2217 Ooij 16	1278 Vagur	1424 Myagmar	0.11	1991		94	95
Uvul	f	Pa	2408 Lelystad 32	915 Apoll	770 Lola	0.14	1992		94	95
Khuskhan	f	Pa	2753 Hustain Nuruu 10	1857 Patron	1814 Zaluu	0.11	1994			
Ov	m	Pa	5041 Hustain Nuruu 42	1846 Paritet	5009 Khuskhan	0.19	1997			
Bor 98	f	Pa	5048 Hustain Nuruu 49	1846 Paritet	2219 Boroo	0.13	1998	May-98		
Uvu 98	f	Pa	5050 Hustain Nuruu 51	1846 Paritet	2408 Uvul	0.12	1998	May-98		
Flicka	f	Pa	5062 Hustain Nuruu 63	1846 Paritet	2217 Tengis	0.19	1998			
Tushig	m	Kh>Pa	5063 Hustain Nuruu 64	1764 Khaan	2183 Naidvar	0.19	1998			
Khu 98	m	Pa	5065 Hustain Nuruu 66	1846 Paritet	2753 Khuskhan	0.19	1998	Jul-98		
Uvu 99	m	Pa	5070 Hustain Nuruu 71	1846 Paritet	2408 Uvul	0.12	1999	Nov-99		
Khu 99	f	Pa	5081 Hustain Nuruu 82	1846 Paritet	5009 Khuskhan	0.19	1999			
Bor 99	f	Pa	5082 Hustain Nuruu 83	1846 Paritet	2219 Boroo	0.13	1999			
Ten 99	f	Pa	5084 Hustain Nuruu 85	1846 Paritet	2217 Tengis	0.19	1999			
Nai 99	m	Pa	5086 Hustain Nuruu 87	1764 Khaan	2183 Naidvar	0.19	1999	Jun-99		
Khu 00	f	Pa		1846 Paritet	5009 Khuskhan		2000			
Ten 00	m	Pa		1846 Paritet	2217 Tengis		2000			
Bayan	m	Ba	1942 Lelystad 20	915 Apoll	770 Lola	0.14	1989		92	98
Meta	f	Tu>Ba	1055 Leipzig 34	383 Roc	563 Medina	0.33	1982	Dec-98	96	96/98
Badmaa	f	Ba	2325 Sprakel 4	1594 Amraa	1555 Nuga	0.20	1992		96	98
Ajarchan	f	Ba	4043 Sprakel 11	1594 Amraa	1612 Salkhi	0.21	1993		96	98
Sharga	f	Ba	2743 Ooij 20	1626 Bohemian	1324 Byamba	0.16	1994		96	98
Sergelen	f	Ba>Ma	2723 Sprakel 17	1594 Amraa	1612 Salkhi	0.21	1994		96	98
Delgerekh	f	Manl>Ma>Ba	2899 Hustain Nuruu 20	1764 Khaan	1912 Belka	0.12	1996			
Zigmee	f	Manl>Ma>Ba	2920 Hustain Nuruu 28	1857 Patron	2086 Tanaa	0.23	1996			
Met 98	f	Ba	5064 Hustain Nuruu 65	1942 Bayan	1055 Meta	0.14	1998	Sep-98		
Marcview	m	Ba	5067 Hustain Nuruu 68	1942 Bayan	4043 Ajarchan	0.23	1998			
Bad 99	f	Ba	5068 Hustain Nuruu 69	1942 Bayan	2325 Badmaa	0.27	1999			
Sha 99	f	Ba	5077 Hustain Nuruu 78	1942 Bayan	2743 Sharga	0.25	1999			
Del 00	f	Ba		1942 Bayan	2899 Delgerekh		2000			
Bad 00	f	Ba		1942 Bayan	2325 Badmaa		2000	Jul-00		
Zig 00	f	Ba		1942 Bayan	2920 Zigmee		2000			
Margad	m	Ma	2701 Hustain Nuruu 8	1857 Patron	2084 Altan	0.22	1994			
Khaan	m	Kh	1764 Lelystad 16	915 Apoll	770 Lola	0.14	1988		92	94
Belka	f	Kh>Mang	1912 Askania 187	821 Parad	1382 Bulka	0.24	1989		92	94
Riska	f	Kh>Ma	1961 Askania 192	970 Paris	1172 Visla	0.40	1990		92	94
Shuurga	f	Kh>Ma	2082 Ooij 6	1278 Vagur	1314 Nyam	0.09	1990		94	95
Svetlaya	f	Kh>Ma>Mang	1978 Askania 212	1159 Perun	765 Vetla	0.30	1990		92	94
Vetochka	f	Kh>Mar>Mang	1970 Askania 203	1159 Perun	490 Vetka	0.36	1990		92	94
Kharzaga	f	Mark>Manl>Ma	2838 Sprakel 22	1594 Amraa	1612 Salkhi	0.21	1995		98	98
Ireedui	f	Kh>Ma	2692 Hustain Nuruu 6	1857 Patron	1890 Hjalgana	0.10	1994			
Tsetseg	f	Kh>Ma	2816 Hustain Nuruu 16	1857 Patron	2086 Tanaa	0.23	1995			
Chotzj	f	Kh>Ma	2912 Hustain Nuruu 21	1764 Khaan	1961 Riska	0.12	1996			
Adzargal	m	Kh>Bach	2915 Hustain Nuruu 24	1764 Khaan	1970 Vetochka	0.13	1996			
Evsel	f	Kh>Ma	5033 Hustain Nuruu 34	1764 Khaan	1978 Svetlaya	0.12	1997			
Balmoral	m	Kh>Bach	5029 Hustain Nuruu 30	1764 Khaan	2082 Shuurga	0.19	1997			
Bernard	m	Kh>Bach	5035 Hustain Nuruu 36	1764 Khaan	1961 Riska	0.11	1997			
Selenge	m	Kh>Ma	5051 Hustain Nuruu 52	1764 Khaan	2692 Ireedui	0.18	1998			
Vet 98	f	Kh	5047 Hustain Nuruu 48	1764 Khaan	1970 Vetochka	0.13	1998	May-99		
Shu 98	m	Kh	5052 Hustain Nuruu 53	1764 Khaan	2082 Shuurga	0.19	1998	May-98		
Bel 98	m	Kh	5058 Hustain Nuruu 59	1746 Khaan	1912 Belka	0.12	1998	Sep-98		
Sve 98	f	Kh	5059 Hustain Nuruu 60	1764 Khaan	1978 Svetlaya	0.12	1998	Jun-98		
Naadam	f	Kh	5061 Hustain Nuruu 62	1764 Khaan	1961 Riska	0.11	1998			
Bel 99	f	Kh	5072 Hustain Nuruu 73	1764 Khaan	1912 Belka	0.12	1999			
Tse 99	f	Ma	5073 Hustain Nuruu 74	1764 Khaan	5015 Tsetseg	0.17	1999			
Vet 99	f	Ma	5074 Hustain Nuruu 75	1764 Khaan	1970 Vetochka	0.13	1999	May-99		
Shu 99	f	Kh	5078 Hustain Nuruu 79	1764 Khaan	2082 Shuurga	0.19	1999	Jun-99		
Sve 99	m	Kh	5079 Hustain Nuruu 80	1764 Khaan	1978 Svetlaya	0.12	1999			
Ire 99	f	Kh	5085 Hustain Nuruu 86	1764 Khaan	2692 Ireedui	0.18	1998	Jun-99		
Ris 00	m	Ma	5088 Hustain Nuruu 89	2701 Margad	1961 Riska		2000			
Ire 00	f	Ma		2701 Margad	2692 Ireedui		2000			
Kha 00	f	Ma		2701 Margad	2838 Kharzaga		2000			
Ares	m	Ar	1891 Koln 25	728 Hubert	1419 Ariane	0.16	1989		96	98
Tsagaan	f	Ar	2013 Howletts 108	1211 Miro	1101 Howletts 43	0.26	1990	Jan-00	96	98
Ayush	f	Ar	2682 Sprakel 15	1594 Amraa	1678 Khavar	0.14	1994		96	98
Khalioen	f	Ar	2729 Ooij 19	1626 Bohemian	1314 Nyam	0.15	1994		96	98
Zeerd	f	Ar	2745 Ooij 21	1626 Bohemian	1462 Argun	0.11	1994		96	98
Caborg	f	Ar	5040 Hustain Nuruu 41	1891 Ares	2745 Zeerd	0.14	1997	Sep-99		
Enkhrlima	f	Ar	5046 Hustain Nuruu 47	1891 Ares	2628 Ayush	0.12	1998			
Aoshka	m	Ar	5053 Hustain Nuruu 54	1891 Ares	2013 Tsagaan	0.17	1998			
Kha 98	m	Ar	5056 Hustain Nuruu 57	1891 Ares	2729 Khalioen	0.16	1998	Feb-99		
Zee 99	m	Ar	5080 Hustain Nuruu 81	1891 Ares	2745 Zeerd	0.14	1999			

Table 2.2. Free ranging harems in HNP. a - This harem was hard released near Enclosure 1. * - These harems were formed by bachelor stallions acquiring mares or dispersed juveniles from the other harems. The bachelors formed a semi-permanent group.

Year of Release	Release enclosure	Stallion		1994	1995	1996	1997	1998	1999	2000
1994	1	Khaan	Mare	4	4	5	8	8	4	
			Juvenile	1	3	3	3	5	1	
			Foal	2	1	3	3	4	2	
			Total harem	8	9	12		18	8	
1994	2	Patron	Mare	5	4	8	9	8	8	8
			Juvenile		3	5	3	2	5	8
			Foal	5	2	2	1	5	3	8
			Total harem	11	10	16	14	16	18	25
1995	1	Paritet	Mare		6	5	4	5	7	7
			Juvenile			1		1	3	6
			Foal				1	2	3	2
			Total harem		7	7	8	9	14	16
1995	a	Turgen	Mare		3	2				
			Juvenile							
			Foal			1				
			Total harem		4	4				
1998	1	Bayan	Mare					5	6	5
			Juvenile					0	1	3
			Foal					1	2	3
			Total harem					7	10	12
1998	2	Ares	Mare					4	4	4
			Juvenile					1	2	4
			Foal					3	2	3
			Total harem					9	9	12
1998	4	Bohemian	Mare					5	2	
			Juvenile							
			Foal							
			Total harem					6	3	
1998	5	Mark	Mare					6		
			Juvenile							
			Foal							
			Total harem					7		
*		Margad	Mare						5	7
			Juvenile						4	4
			Foal						1	3
			Total harem						11	15
*		Manlai	Mare					6	3	
			Juvenile							
			Foal							
			Total harem					7	4	
*		Mangir	Mare						3	3
			Juvenile							3
			Foal						2	1
			Total harem						6	8
		Bachelors				4	5	8	6	7

moved to be with the bachelor stallion Mangir, leaving Khaan alone. Svetlaya and Vetochka then joined Belka and Mangir leaving the rest of the mares and their offspring with Margad. Khaan roamed alone and with the bachelor group until his death in the winter of 2000.

2.2.1.2 Paritet

Paritet was transported to Mongolia in 1992 and was kept in Enclosure 3 with other bachelors until 1995, when he was put in Enclosure 1 with five mares (Naidvar, Boroo, Buyana, Tengis and Uvul) who arrived in Mongolia in 1994. They were released later in 1995. Khuskhan dispersed from Patron's harem to Paritet's in 1996 and had the first foal of this harem in 1997 (Ov). Until 1998 only two foals survived out of ten born since 1995, but in 1999 and 2000 there was greater success as five out of the seven foals born survived. Naidvar joined Khaan's harem in 1997, but returned to Paritet early in 1999 with her yearling. Ayunga joined Paritet's harem in 1999. She had arrived with Bohemian's harem in 1998 and they were released after acclimating for 4 months. All the other mares died from the tick-borne blood disease babesiosis, and Bohemian was herded into an enclosure after he became extremely weak from this disease.

2.2.1.3 Bayan

Bayan arrived in Mongolia in 1992 and was kept with other bachelor males in Enclosure 3. In 1996 he was put with the mares Badmaa, Sergelen, Sharga and Ajarchan in Enclosure 1 after their stallion died shortly after their arrival in that year. Meta was originally released with Turgen in 1996, but was put in the enclosure with Bayan after Turgen died in 1997. Sharga jumped out of the enclosure in July 1996 and joined Patron until 1997. After moving between bachelors and Turgen she was herded into the enclosure along with Meta. Bayan's harem was released in May 1998.

The mares Delgerekh and Zigmee joined Bayan's harem in June 1999. They had dispersed from Khaan and Patron's harems respectively in 1998 and joined the bachelor stallion Manlai (Delgerekh's full brother) with Kharzaga. After Manlai was injured in a fight all three left and joined Margad's harem. Delgerekh and Zigmee stayed for less than a week, but Kharzaga remained there. Kharzaga had been released in September 1998 after acclimating for four months with Mark's harem. Delgerekh and Zigmee moved on to Bayan's harem where they have stayed, despite a brief

sojourn by Zigmee, Ajarchan and her yearling to Margad's harem. Sergelen left Bayan and joined Margad's harem in May 2000.

2.2.1.4 Margad

The formation of Margad's harem is included in the above.

2.2.1.5 Ares

Ares and the mares Tsagaan, Ayush, Khalioen, and Zeerd were brought to Mongolia in 1996 and placed in Enclosure 2. One foal was born in the enclosure in 1997 and three in 1998. One of the '98 foals died after release in February 1999. The gates of the enclosure were opened in August 1998, but the horses did not leave for a month. After their initial foray outside the enclosure they appeared to use it is a base for further occasional explorations around the reserve. In 1999 and 2000 the horses remained almost entirely within the enclosure so they were not studied. Late in 2000 the fence was dismantled.

2.3 Behavioural observations

Scan sampling (the activity of an individual or harem recorded at a preselected moment in time) and all-occurrence sampling (all occurrences of a certain behaviour or activity recorded) methods (Altmann, 1974) were used for observing behaviour. In 15 months of fieldwork, five harems were observed for a total of about 860 hours. The horses were not observed year round due to limited time and money available for field studies. The different harems were not observed for the same length of time due to unforeseen circumstances in the field (observation hours of each harem are presented in Appendix II). The standard observation procedure was that a harem would be found at or close to dawn and then followed until 1400h. The same harem was then found at 1400h the next day and followed until dusk. In this way observations of the harems were made from dawn to dusk. In 2000, one harem (Paritet's) was also followed at night, but only home range and habitat use data were recorded. The horses could normally be watched on foot from a distance of about 15m once they were accustomed to the presence of the observer. All animals were identified by coat colour and markings, tail length and mane fall and length.

Home range and habitat use data were recorded on a data sheet. They were then entered in to the database in the GIS (Geographical Information System) programme Arcview. The tabulated data were exported to Excel for further manipulation and analysis. Other behaviour data were recorded on to a micro-cassette recorder and then transcribed on to an Excel spreadsheet.

Mongolian rangers and biologists gathered the data between December and March, and from 1995 to 1997. These data were only used for the analysis of home ranges and habitat use.

2.3.1 Scan sampling

2.3.1.1 Ten minute scan sampling - Home range and habitat use

The following were recorded every 10 minutes throughout each observation session:

- Time
- Position – The position of the harem was plotted on a large-scale topographical map of the reserve. In addition, the position was found using a Garmin GPS 12 Global Positioning System (GPS) every time the horses moved. To support the information the error displayed by the GPS and the estimated distance and direction of the horses from the observer were recorded.
- Activity – The behaviour which most of the harem was doing was recorded. If exactly half the harem was performing a particular behaviour the activity of the majority immediately before or after the sample point was used. The following behavioural acts were recorded (after Boyd and Houpt, 1994):

  Grazing – The horse has its head to the ground and is plucking the vegetation or chewing. If the horse is moving while chewing this was recorded as grazing.

  Recumbent rest – Lying down, either lying on the sternum or flat on the side.

  Moving – Any form of locomotion.

  Standing – No locomotion, but no resting posture exhibited.

  Stand resting – No locomotion but with at least two of the following four features seen:

  One back leg flexed;

  Drooping lower lip;

  Ears to the side and partly lowered;

  Eyes partly or completely closed.

Other – If the majority of the horses did not fall in to any of the above categories.

Out of sight – The majority of the harem could not be seen.

In 2000 the behaviour sampling protocol was changed. As well as the above, the activity of every horse within the harem was recorded, and more behavioural acts were identified and recorded:

Browsing – Feeding on shrubs or trees rather than grass.

Drinking – Mouth held to the water.

Lying laterally – Lying flat on the side with the head touching the ground.

Lying sternally – Lying on the sternum with the head up or resting on the front teeth and the legs flexed.

Mutual grooming – Standing head to tail with another horse chewing each other's coats.

Self grooming – Rubbing against an object, using the teeth or hoof to scratch or rolling on the ground.

Nursing – The foal has its head under the mothers flank and nose to the udder. This was recorded for both mother and foal.

- Wind speed –In 1998, the wind speed was subjectively coded:

  1 – None

  2 – Apparent only

  3 – Grass and forbs bend

  4 – Tree branches bend

  5 – Trees bend

In 1999 and 2000 a digital Silva 'wind watch' anemometer was used. It was held in the direction of the wind for 20 seconds and the average wind speed displayed was recorded.

- Wind direction – The direction of the prevailing wind was found using a compass.
- Temperature – This was measured in degrees centigrade on a thermometer kept in the shade.
- Cloud cover – This was estimated cover of the sky in tenths.
- Precipitation – This was subjectively recorded as:

  0 – None

  1 – Light rain

  2 – Steady rain

3 – Heavy rain

4 – Sleet

5 – Snow flurries

6 – Heavy snow

7 – Hail

8 – Other

9 – Fog

- Comfort behaviour – This was an estimation of how much the majority of the harem were bothered by flies (after Mayes and Duncan, 1986). In 2000 this was also recorded for each individual:

  0 – None

  1 – Some tail swishing

  2 – Constant tail swishing and some head shaking

  3 – Constant tail swishing and head shaking, some stamping

  4 – Constant tail swishing, head shaking and stamping, rubbing, rolling and other signs of distress.

2.3.1.2 Bite rate

Bite rate was examined to show any differences in the nutrition of the different vegetation classes and any differences in the consumption of horses of different ages and sexes. If the horses grazed for longer than 20 minutes, the bite rate was recorded for one minute every subsequent 20 minutes while grazing. A horse was chosen at random (without replication until all horses had been sampled within one observation session) and the number of bites that it took within one minute was counted (after Putman, 1986). In 2000 the number of steps that the horse took was counted along with the bites. Foals were not sampled.

2.3.1.3 One minute scan sampling

2.3.1.3i Associative behaviour

Associative behaviour is all social behaviour conducted between horses that is not agonistic. The following behaviours were recorded in addition to the ten minute scans. In 1998 all occurrences of the behaviours were recorded, plus the duration of mutual grooming bouts. In 1999 and 2000 the harem was scanned every minute for:

- Mutual grooming – Reciprocal coat care where the horses stand head to tail and chew or nuzzle each others coats (Boyd & Houpt, 1994) (Plate 2.1). The names of the horses grooming each other were recorded along with the initiator, if seen. The part of the body groomed was also recorded.
- Stand resting together – Occurs when the horses are stand resting (as per the criteria above), but are standing head to tail within one metre of each other (Plate 2.2). The names of the horses stand resting together were recorded.
- Play – Both play by self and playing with another were recorded. Play is a behaviour with no other perceived function (Boyd & Houpt, 1994), and could be distinguished from agonistic behaviour as the ears were held forward or laterally, rather than back. The name(s) of the horse(s) playing was recorded.
- Head rubbing – When one horse rubs or leans its head on another without eliciting an aggressive response. The names of both horses were recorded.

2.3.1.3ii Vigilance behaviour

Three behavioural postures were recorded to represent vigilance behaviour. These were:

- Look – the horse raises its head no higher than it would be held for walking on level ground and points both ears in the direction it is looking (Plate 2.3a).
- Stare – the horse lifts its head higher than for looking but not as erect as standing alert and both ears are pointed in the direction it is looking (Plate 2.3b).
- Stand alert – the horse lifts its head fully erect and focuses its eyes and ears in one direction (Plate 2.3c).

In 1998 all occurrences of standing alert by each horse were recorded along with the stimulus (i.e. what the horse appeared to be looking at) and the length of time the horse maintained this posture. The sequence of events (what the horse did before and after standing alert) was also recorded. Look and stare were not recorded in 1998. As standing alert was quite a rare behaviour, in 1999 and 2000 it was decided to scan sample for vigilance every minute and include look and stare. The time, name of the individual displaying a vigilance behaviour and the stimulus apparently being looked at were recorded.

Plate 2.1. Buyana (left) and Naidvar mutual grooming.

Plate 2.2. Stand resting together.

Plate 2.3. Different levels of vigilance.

a). Paritet looking.

b) Margad staring.

c) Margad standing alert

2.3.2 All-occurrence sampling

2.3.2.1 Agonistic behaviour

Agonistic behaviour is all aggressive interactions between horses. In 1998 agonistic events were recorded to the nearest minute; in 1999 and 2000 to the nearest second. The name of the aggressor and recipient of aggression and the outcome of the event were recorded, plus the behaviour used by the aggressor and any retaliation by the recipient. In the case of a fight of a longer duration between horses the full sequence of events was recorded.

The following agonistic behavioural acts were recorded (after Boyd and Houpt, 1994):

- Bite – Head and mouth extended with ears laid back and connection made between the teeth/mouth of the aggressor and the recipient.
- Bite threat – As above but the head is simply moved in the direction of the other horse without contact. The movement can be slight (Plate 2.4) or overt.
- Bite threat and chase – As above but the aggressor moves towards and runs after the recipient.
- Herd – Usually conducted by the stallion. The head is held low to the ground with the ears laid back and is sometimes moved in a 'snaking' manner (Plate 2.5).
- Hind leg kick – One or both back legs are thrust out and connect with another horse.
- Hind leg kick threat – As above but no contact is made. The movement can be fully followed through or simply the back leg can be lifted slightly while the ears are laid back.
- Snap – Usually performed by younger animals. The head is often extended and the mouth is opened and closed with the lips retracted.
- Strike – A fast out and down movement of a fore leg.
- Other – Any combination of the above behaviours.
- Move – The recipient of aggression moves away from the aggressor.
- Not move – The recipient of aggression does not move.
- Not move and aggress - The recipient of aggression does not move and returns aggression.

Plate 2.4. Mild bite threat evoking a large response. Buyana (left) to Uvul. Photo: T. Roos.

Plate 2.5. Margad herding.

2.3.2.2 Marking behaviour

Marking behaviour was defined as when a horse sniffed a non-food item and then proceeded to either flehmen, urinate or defecate. The time that the marking occurred and the name of the animal marking were recorded. The sequence of behaviours used to mark were noted (e.g. whether the stimulus was sniffed before marking, after or both, and what form the marking took), along with the stimulus marked and the terrain where the marking occurred. If the marking happened during or after a confrontation with another horse this also was recorded.

Stud piles were surveyed whenever they were encountered. A stud pile was where at least two dungings had occurred on the same spot. The longest width, length and height of the stud pile was measured and its age was estimated as either fresh, new, old, new on old, fresh on old, or fresh on new. The position of the stud pile was noted on a large scale map and entered in to Arcview with its details and the name of the horse seen marking it, if this was observed.

2.3.3 Fly sampling

Two methods were used to examine the flies in the home ranges of the study harems: fly traps, and flies counted on a horse. Fly traps were used to find what species were present, and flies were counted on a domestic horse to find the abundance of flies in different parts of the home ranges of the harems.

2.3.3.1 Fly traps

In 1998 locally made sticky traps were used - 26 x 17.5cm pieces of paper covered with adhesive. This was attached to the top of a 1.2m stick and erected near the horses, in similar conditions, throughout the observation period. It was examined every 30 minutes for flies, which were then removed with forceps, and descriptions of each type noted. These traps proved to be very inefficient as they only caught flies during five sampling sessions in July and August. They were also difficult to use in the field. Therefore water traps were used in late 1998 and in 1999. These were 20 x 12 x 8 cm white trays that were filled with water to a depth of 2.5 cm with a drop of detergent on top. They were then left for at least three hours in grazing and resting places used by the horses. The flies caught were noted and samples of each type were removed and preserved in alcohol. This was repeated at least twice a month. The

preserved flies were brought back to London and identified to the family level with the aid of keys by Oldroyd (1954) and Chinery (1993).

2.3.3.2 Fly counts

A domestic horse was ridden to the resting sites and grazing sites where the fly traps had been set (after Duncan, 1983). All fly count samples were taken between 0800h and 1400h and took place once a week throughout the study periods in 1998 and 1999. At each site the horse was stopped for 10 minutes before the flies were counted on each side of the horse (separated into areas in front of the saddle, i.e. neck/shoulder, and behind the saddle, i.e. haunch) and its head. Flies on the legs and those hovering around the horse were not counted. Weather conditions, the colour of the horse and its activity while the flies were counted were noted.

2.4 Data analysis

There were different numbers of horses in each harem and in each year, and the harems were observed for different numbers of hours over the period of study. The number of hours the horses were observed also varied with the different months due to the longer hours of sunlight in summer. However the observation period between dawn and dusk was almost the same for each harem within each month of the year that they were studied (Appendix II). The 'dawn to dusk' or 'standard' day was therefore used as the standard observation period for analysis.

The Kolmogorov-Smirnov test was used to test for normality of all data before analysis. However, most data were not normally distributed and for the most part non-parametric tests such as Kruskal-Wallis ANOVA, Friedman's ANOVA, Mann-Whitney U test and Spearman's rank correlation have been used (Siegel & Castellan, 1988). Tukey's post-hoc tests for Kruskal-Wallis were used to reveal which medians were significantly different from each other (Siegel & Castellan, 1988). Unless stated otherwise, all Kruskal-Wallis results were adjusted for ties. Where data were normal, the appropriate parametric test was used. Most statistical tests were carried out using the software packages Minitab for Windows 12.1 and StatsDirect version 1.617. Other tests used are described below.

2.4.1 Home range and habitat use

The home range and habitat use data were analysed using the GIS programme Arcview 3.2 (ESRI, 1998). An application within Arcview called the Animal Movement extension (Hooge & Eichenlaub, 1997) was used to find the home range area in all cases. The home ranges were analysed using the fixed kernel method, which was found to be most accurate by Seaman and Powell (1996). This method consists of superimposing a grid on the set of sample points (fixes). An estimate of the density of the sample points is obtained at each grid intersection using information from the entire sample, providing an average of the densities of all kernels that overlap that point. Observations close to the intersection will contribute more to the estimate than observations that are far from it. Thus, the density estimate will be high in areas with many observations, and low in areas with few (Seaman & Powell, 1996). The smoothing parameter used to determine the width of the kernels was the Arcview default value. This was found to provide a good estimate of home range size (Hooge & Eichenlaub, 1997). Utilisation curves were created to find the core area of each harem in each year (Appendix III).

It was hypothesised that home range sizes would be larger when harems had been free ranging for longer and when there were more horses in a harem and these assumptions were explored using Pearson's correlation coefficient. The degree of overlap within and between the harems was also expected to have been affected by time since release; this again was explored using Pearson's correlation coefficient, and differences in the size of the overlap was tested with ANOVA. Range shifts were examined by comparing the overlap within a harem's home range over the years since release, and also by examining the distance between the centre (arithmetic mean of all points) of home ranges across the years. Kruskal-Wallis and Spearman's correlation coefficient tests were used to explore the use of the horses' home ranges in the different seasons and at different temperatures, because it was assumed that they would use different elevations in the different seasons and for different activities.

2.4.2 Time budgets

The time budgets of the horses were extrapolated using pivot tables in Excel. Differences among the harems, and differences in the activities of the harems in the different hours of the day and months were tested using Kruskal-Wallis ANOVA. The effects of factors such as the number of new horses, the number of juveniles, the

number of horses in the harem, the number of foals and the number of years since release on the frequency of grazing, moving and stand-resting were explored using Pearson's correlation coefficients (as these data were normal). The individual time budget data collected in 2000 were used to find the effect of age and sex, and lactation and/or pregnancy on the frequency of each behaviour. Differences in the relative frequency of these behaviours were examined using two-way ANOVA and Pearson's correlation coefficient was used to explore the effect of other environmental factors.

The synchronisation of behaviour within the time budget of a harem was analysed from individual time budget data collected in 2000. A synchronisation index was formed by counting the maximum number of horses performing the same behaviour at each sample point (i.e. at one sample point, in a harem of 10 horses, if 6 were grazing, 3 were stand-resting and 1 moving, a score of 6 was recorded). This figure was then divided by the number of horses in the harem to provide a synchronisation score (1/n to 1 (all animals synchronous)).

To examine whether the behaviour of offspring was affected by their mother or sibling, every observation of each mother-offspring dyad, (foals and juveniles were analysed separately), was examined to see if they were doing the same behaviour. They were scored 1 if both were performing the same behaviour or 0 if it was different. Samples where one or both animals were out of sight were excluded from the analysis. When analysing mother-foal dyads, samples where the foal was lying down were also excluded as foals spent more time lying down than their mothers, therefore biasing the end value. To test whether the harem was synchronous with the stallion a score of 1 was given when the majority of the harem was performing the same behaviour as the stallion, and a 0 if the behaviour was different. Kruskal-Wallis ANOVAs were used to test for any differences among the harems, and for differences in synchronicity through the day. Unpaired t-tests were run on the means of the mother-offspring, sibling and stallion data to examine any differences compared to the mean of the harem as a whole.

2.4.3 Vegetation use

A vegetation map was digitised into Arcview by the Information and Computer Centre, Mongolian Ministry of Nature and Environment, 1999. It was therefore possible to find the vegetation types where each of the observations of grazing occurred, as well as the area covered by the vegetation types within each home range.

The vegetation types from the map were classified into the 11 vegetation classes found in HNP by Wallis de Vries *et al.* (1996). Selection for different vegetation classes was then examined using the method in Manly *et al.* (1993) for data with known proportions of available resource units. The vegetation selection of each harem in each year was analysed using all points where grazing was observed in 100% fixed kernel home ranges over one sampling year. The seasonal use of vegetation was examined by using all points where grazing was observed in each season of all years the horses were watched, to maximise the sample size. This was then compared with their total range over all years to provide an area of vegetation available to them. The year was divided into seasons according to the Mongolian weather: spring – March to May, summer – June to August, autumn – September to November, and winter – December to February. Sample sizes were very small for the winter (a total of 61 points where grazing was observed in two harems).

After Manly *et al.* (1993), the selection ratio (w_i) was calculated for each vegetation class i by

$$w_i = o_i/\pi_i$$

where o_i = proportion of observed grazing on vegetation class i and π_i = the proportion of area covered by vegetation class i within the harem's home range (defined by a 100% kernel). A value of $w_i = 1$ indicates no selection of that vegetation class, $w_i < 1$ indicates avoidance, $w_i > 1$ indicates attraction or preference. This selection ratio was then standardised to give B_i, the estimated probability that a randomly selected vegetation class will be used if all classes are equally available:

$$B_i = w_i/(\sum_{j=1}^{I} w_j)$$

B_i will have a value between 0 and 1, indicating relative selection of a vegetation class. A Chi-squared test was used to test the null hypothesis that the harems were randomly selecting vegetation classes in proportion to their availability.

$$X_L^2 = 2 \sum u_i \log_e\{u_i/(u+\pi_i)\}$$

where u_i = vegetation use (number of observations in that vegetation class) and u_+ = the total number of observations. The standard error (se) and confidence intervals of the proportion of observed grazing on each vegetation class (o_i) were then calculated:

$$se(o_i) = \sqrt{\{o_i(1-o_i)/u_+)\}}$$

$$o_i \pm z_{\alpha/2}\sqrt{\{o_i(1-o_i)/u_+\}}$$

A Bonferroni correction was used. If the value of α is set at 5%/I then there will be a probability of about 0.95 that all confidence intervals will include their respective population ratios.

The significance of the selection ratio (w_i) for each vegetation type was tested by seeing if the confidence interval contained 1,

$$se(w_i) = se\ (o_i/\pi_i) = \sqrt{\{o_i(1-o_i)/\pi_i^2)\}}$$

$$w_i \pm z_{\alpha/2}\ se(w_i),$$

and by comparing $(w_i-1)^2/se(w_i)^2$ with critical values for the Chi-squared distribution with one degree of freedom.

The validity of the confidence intervals and the Chi-squared tests was dependent on there being five or more observations in each vegetation class. Where this requirement was not met the results were taken as indicative only.

The bite rate among the ages and sexes was examined using a Kruskal-Wallis test. It was expected that lactating or pregnant mares would have a higher bite rate than those without a foal and this was tested with a Mann-Whitney U test. The bite rate in the different vegetation classes was also examined.

2.4.4 Agonistic behaviour

Behavioural acts that were observed on two occasions or less were not used in the analysis. The standard day was used as a replicate. To take into account the different harem sizes, the data were expressed as the relative frequency of each behavioural act per horse (by taking the results and dividing by the number of horses in the harem). The data sets contained many zeros and were not normally distributed. Kruskal-Wallis

tests with results adjusted for ties and Chi-squared tests were therefore used to analyse the data. The data were analysed with respect to year, harem, sex and age for both the aggressive and retaliatory behaviour.

A dominance hierarchy was drawn up for each harem in each year by plotting the winner and loser of every interaction in a matrix. All interactions in which there was a clear winner were used (if the recipient of aggression moved it was taken to be the loser of that interaction). Interactions in which the recipient of aggression did not move, or the aggressor moved, were not used, as the relative dominance of the two individuals could not be identified. Sexual behaviour was not used. Foals were not included in the dominance hierarchies as interactions with and among them were rare.

The rank order of these matrices was calculated using the I & SI method (de Vries, 1998). This is an iterative procedure that minimises the number of inconsistencies (I) in the ranking order and minimises the total strength of any inconsistencies (SI) in the matrix. An inconsistency was when one individual dominated another, while being below it in the rank order, and the strength of an inconsistency was the difference in rank positions between the individuals involved. The first phase of the I & SI method was an iterative procedure in which the positions of each dyad were switched (the generalised (heuristic) swapping rule) until the fewest inconsistencies possible, and of the least strength, were obtained. One hundred sequential tries of the matrix set in a random order were run, until the matrix with the lowest number of inconsistencies was produced (Appleby, 1983). In the second phase, individuals which had an undecided relationship with other individuals adjacent to them were ordered. An undecided relationship was when a relationship was tied or unknown (no observed interactions). The most dominant individual in one of these relationships was the one that was most successful, i.e. had the greater value of D – S, where D is the number of individuals dominated and S is the number of individuals by which it is dominated (Noldus Information Technology, 1998). MatMan Version 1 for Windows (Noldus Information Technology, 1998), a computer programme for the analysis of sociometric matrices, was used for all calculations.

The final rank order is only accurate when there is a linear rank order of animals (Appleby, 1983), which was not always the case here, probably due to the number of unknown relationships. The linearity of the matrices were analysed using Landau's linearity index (h):

$$h = \frac{12}{N^3 - N} \Sigma [V_i - (N-1)/2]^2$$

where V_i is the number of animals dominated by the individual i, and N is the number of individuals. A linearity index which corrects for unknown or tied relationships within the matrix (h') was also used (de Vries, 1995):

$$h' = h + \frac{6u}{(N^3 - N)}$$

where h is the value of Landau's h calculated for the dominance matrix in which the unknown dyads have been assigned the value ½ (according to the procedure of Appleby, 1983), u is the number of unknown dyads (assigned the value zero), and N is the number of individuals (Noldus Information Technology, 1998). As all matrices contained unknown relationships the linearity index h' was used here. To assess the statistical significance of the degree of linearity h' a two-step randomisation process test was performed (de Vries, 1995). This involved constructing a matrix in which all unknown relationships were randomly changed into 1-0 or 0-1 dyads, and the number of circular triads (d_0) was calculated. If all relationships were known, d_0 is one of the possible values of the number of circular triads in the randomised matrix. The dominance relationship within each dyad was then randomised, and the number of circular triads in this matrix (d_r) was calculated (de Vries, 1995). This was then repeated 10 000 times and the left tailed probability (p) of d_0 was calculated as:

$$p = \frac{\text{Number of times that } d_r \leq d_0}{\text{Number of randomisations.}}$$

A directional consistency index (DC) was used to show in which direction behaviours were performed:

$$DC = \frac{(H - L)}{(H + L)}$$

where DC is the total number of times behaviour occurred in the direction of the higher frequency, H, minus the number of times in the less frequent direction, L, was divided by the total frequency. The DC index ranges from 1 (where all aggression is

directed from dominant to subordinate animals or vice versa) to 0 (where there is an equal exchange) (van Hooff & Wensing, 1987).

2.4.5 Associative behaviour

As a result of the low sample size, data from all years and all harems have been combined for the analysis of the frequency of associative behaviours. Only mutual grooming and stand resting together at the harem level have been analysed. The other behaviours, head rub and play, were very rare. The data were analysed per minute of each standard day as described above for agonistic behaviour. Chi-squared tests were used to find if the hour and month affected the frequency of the behaviours; Kruskal-Wallis ANOVA was used to test for differences among the harems. In the case of mutual grooming, the body part most groomed was also found. Any correlation between relatedness (the coefficient of relatedness 'r') and the frequency of associative behaviours was worked out for each harem. Correlations were also run to explore possible effects of aggressiveness, total relatedness, age and tenure in the harem on associative behaviour.

2.4.6 Marking behaviour

Marking behaviour was observed on all but four of the standard days. However, the data set was relatively small so the years were combined for analysis and all data were analysed using Chi-squared tests. Differences in the frequency of marking by the different stallions, and in different months were analysed as well as where most marking took place – the stimulus and terrain, and the form the marking took. The type of terrain where each stimulus occurred and changes within the year were also examined. The sequence of events in the ritual of marking were analysed to see if the horses sniffed most before or after marking, and if this was affected by the stimulus. The situation of stud piles was examined by comparing their position within the home ranges and core area of the harems in Arcview.

2.4.7 Vigilance behaviour

The vigilance data were analysed per minute of each standard day per animal in each harem. The data were then analysed by Kruskal-Wallis tests with respect to harem, time of day, month. Chi-squared tests were used to find associations among age and sex, and stimuli causing vigilance. Differences between horses within a harem were

examined using Kruskal-Wallis tests. Any correlation between vigilance and factors such as age, dominance rank, tenure in the harem and size of the harem were found using Spearman's rank correlation. Differences in the frequency of the three vigilance behaviours, and the stimuli causing them were examined.

2.4.8 Fly data

The fly trap data were used to find which families of flies were most abundant, and where (using Chi-squared tests and diversity indices), and to explain the effect that these flies had on the horses. Some families of flies contained 'types', which are likely to equate to species. Insects that were not removed from the traps were assigned to a family based on the description, resulting in a known total of the number of flies caught, and the possible maximum number that includes those not removed for each family. The diversity of types of fly in the different trapping areas were analysed by the Shannon-Wiener diversity index:

$$H' = \sum_{i=1}^{s} (p_i)(\log p_i)$$

where H' = index of species of diversity, s = number of species, and p_i = proportion of total number belonging to *i*th species (Krebs, 1989). H'_{MAX} was calculated by log S (S = number of types caught) for comparison. The evenness of the type diversity (J') was measured by:

$$J' = H'/ H'_{MAX}.$$

The fly count data were analysed with Chi-squared tests, Kruskal-Wallis tests and correlations to examine the effect of month, weather conditions or colour of horse on the abundance of flies. Differences in the abundance of flies in the different parts of the home ranges were analysed. The effect of flies on the Przewalski horses was analysed, using similar tests, by looking at the effect of factors such as weather and elevation, on their comfort behaviour (recorded every 10 minutes during observations).

Chapter Three

Home range and habitat use

Chapter 3. Home range and habitat use

3.1 INTRODUCTION

3.1.1 Home range

The home range of an animal contains everything that it requires in its daily life, and so attaining knowledge about an animal's home range will enable us to get a better understanding of its behaviour. In the case of a reintroduced animal, this information carries an added importance as the pattern of movement from acclimatisation enclosures and the establishment of home ranges can be used to help assess how future reintroductions may proceed. After release, knowledge of the habitat that an animal is likely to select will enable its movements to be predicted. Management decisions on issues such as the potential carrying capacity of the release site can be made from data of the home range size of the animals and their habitat requirements. In the case of the Przewalski horse nothing is known about its home range size or its social structure in the wild, but information about feral domestic horses and wild equids may be helpful as baseline information. It is particularly important to have an idea of how the new population of Przewalski horses is likely to spread through the release site and what the carrying capacity of the reserve might be. A potential problem, for example, is that domestic horses, with which the Przewalski's can hybridise, are present outside the boundaries of the reserve.

Wild and feral equids have home ranges of between 1 and 600 km^2 (Table 3.1), although the very large home ranges for plains zebras also include their migration routes. It appears that one of the main factors affecting home range size is the environment: horses living in harsher environments with poorer vegetation tend to have larger home ranges. Thus horses in the temperate grasslands of England have a maximum home range of 10.2 km^2 (Gates, 1979; Tyler, 1972), whereas in the arid Red Desert, home ranges can be 30 times as large (Miller, 1983b). It was expected that the Przewalski horses at HNP would have home ranges similar to those seen in the comparable habitat of the arid shrub steppe lands of the western United States (up to 48 km^2). In several studies (Berger, 1977, 1986; Gates, 1979; Linklater *et al.*, 2000;

Table 3.1. Size and use of equid home ranges in the literature.

Species	Population	Home range size (km^2)	Seasonal change	Home range overlap	Method of home range analysis	Reference
Equus przewalskii	HNP, Mongolia	1.3 - 24.0	Winter > Summer*	Yes	Fixed kernel	This study
E. caballus	Grand Canyon, USA	8 – 48	Winter > Summer	Yes	~ MCP	Berger, 1977
	Pryor Mountain Range, USA	3 – 32		Yes		Feist & McCullough, 1976
	Red Desert, USA	73 – 303	Largest spring / autumn	Yes	Minimum home range (Mohr, 1974)	Miller, 1983b
	Wassuk Range, USA		Yes	Yes[a]		Pellegrini, 1971
	Great Basin, USA	4.4 – 35.6	Largest in summer	Yes	~ MCP	Berger, 1986
	Shackleford Banks, USA	3 – 6		No		Rubenstein, 1981
	Assateague Island, USA	2.7 – 11.4	Winter < Summer	No & Yes		Zervanos & Keiper, 1979
	Chincoteague Island, USA			Yes		Keiper, 1976
	Alberta, Canada	2.6 – 14.4		Yes		Salter & Hudson, 1982
	Exmoor, UK	2.5 – 3.2	Winter < Summer	Yes	~ MCP	Gates, 1979
	New Forest, UK	0.8 – 10.2	Yes	Yes		Tyler, 1972
	Camargue, France		Yes	No to Yes[b]		Duncan, 1992
	Toi Cape, Japan		Yes	Yes		Kaseda, 1983a
	McDonnell Ranges, Australia			Yes		Hoffmann, 1983
	Kaimanawa Range, NZ	1 – 17.7	Winter > Summer	Yes	MCP	Linklater *et al.*, 2000
E. africanus	Chemehuevi Mountains, USA	4 – 97		Yes[c]	~ MCP	Woodward, 1979
	McDonnell Ranges, Australia			Yes		Hoffmann, 1983
	Danakil, Eritrea	12 – 40		Territory		Klingel, 1977
E. hemionus	Negev desert, Israel	17 ± 11		No[d]	Fixed kernel	Saltz *et al.*, 2000
E. zebra	South Africa	3.1 – 16		Yes		Penzhorn, 1982b
E. quagga	Ngorongoro, Tanzania	80 – 250	Yes	Yes		Klingel, 1969
	Serengeti, Tanzania	3 – 600	Rain < Dry	Yes		Klingel, 1969

Blank spaces indicate that information was not present in the paper cited. Home range sizes are of the entire range, or the largest figures given (90% or 95% home range). Relative size of the range in the different seasons is given, or if there is a difference. Methods for analysis of home range are as described in the papers: MCP = Minimum Convex Polygon; ~MCP = figures in the paper, or methods used, appear to approximate a MCP, but no details are given. * - This was not a significant relationship, but a trend was shown. [a] - home ranges are said to overlap in the text, but appear to only marginally overlap in the diagram of home ranges, [b] - home ranges overlapped as the population increased, [c] – one male described as having a territory, [d] - male home ranges only.

Miller, 1983b; Zervanos & Keiper, 1979) there was a tendency for a seasonal change in range size. The studies where the winter ranges were larger than the summer (Berger, 1977; Linklater *et al.*, 2000) occurred in areas with strong seasonality and a relatively short growing season. In contrast the two studies where the winter ranges were smaller than the summer (Gates, 1979; Zervanos & Keiper, 1979) occur in places where the seasons are less extreme. This suggests that large winter ranges might be necessary to provide enough forage and places to shelter. Miller (1983b) recorded largest ranges in the spring and autumn, which could also be due to the need to find large amounts of forage in these seasons. However the pattern is not straightforward, as horses in the Great Basin, which has very cold winters and hot summers, had largest home ranges in the summer (Berger, 1986), although again, this could be due to the pattern of vegetation or other resources such as water. The growing season for vegetation in Mongolia is from May until September. After September the grass is killed, but effectively freeze dried by the sudden chill and may be covered by snow during the winter months. This change in the quality of food must also affect the ranges of the horses.

The main requirements in the home range of a horse are sufficient forage, water, shelter from the weather and shelter from flies (Tyler, 1972). There are no clear patterns of water use among equids as its availability varies among the studies, and the frequency of drinking will vary with physiological need and closeness to water (Waring, 1983). Studies on feral horses in America have shown that all home ranges include a water source, often forming the point of overlap between home ranges (Feist and McCullough, 1976; Pellegrini, 1971). This is clearly an important factor when choosing a release site. Different populations have different drinking schedules; on Assateague Island in America the horses tended to drink around dawn or dusk (Keiper & Keenan, 1980), but in other studies they have been observed to stay near water all night (Pellegrini, 1971), or else drink at intervals during the day (Feist & McCullough, 1976). These patterns will change with the season, as in the summer the horses will need to drink more to replace water lost as sweat, and in the winter they can consume snow and so do not need to seek a water source. In summer horses drink at least once a day, and may travel far to do so, (seven miles (11 km) being recorded by Pellegrini (1971), and female Asiatic asses were observed to travel a round trip of 40 km to and from water (Saltz *et al.*, 2000)), but if they remain near water they will drink more often (Waring, 1983). Other factors will also affect when the animals drink. Joubert

(1972) found that 'disturbed' mountain zebras tended to drink more at night, whereas 'undisturbed' zebras drank during the day as well.

Shelter from flies in summer is probably as important for horses as shelter from the weather in winter, and will also affect their behaviour. Horses stand rest, normally in groups, and whisk flies away with their tails in the summer, when fly abundance is at its peak. They are able to devote more time to this activity and less time to feeding due to the availability of relatively high quality forage between spring and autumn. Fly avoidance behaviour will be affected by the horses' need to move to places where they can regulate their body temperature. Horses have been observed to use ridges and bare ground or snow patches to shelter from flies (Keiper & Berger, 1982). To shelter from inclement weather, horses have been observed to select habitat such as slopes facing the sun in New Zealand (Linklater *et al.*, 2000), and more sheltered inter-dune habitat on Assateague Island (Zervanos & Keiper, 1979). In the Great Basin horses were observed spending more time at low altitudes through the winter (Berger, 1986), and Miller (1983a) found that distance from ridges, along with distance from water and forage, affected the seasonal distribution of horses.

3.1.2 Time budgets

Horses have been shown to have a definite pattern of behaviour through the day in all studies (Tables 3.2a and 3.2b). Horses tend to graze more in the morning and evening, rest through the middle of the day, and lie down between 0200h and 0400h. This pattern varies with the season (Table 3.2a). In the winter horses usually spend less time resting during the day and more time grazing (Keiper *et al.*, 1980). Przewalski horses show this same pattern of behaviour in captivity, although it is affected by enclosure size (Boyd *et al.*, 1988). Przewalski mares spent more time stand resting when they were kept in a large yard than when they were on pasture, and in general captive Przewalski horses spend less time feeding than feral domestic horses (Table 3.2b).

Time budget data about feral or wild equids, and a comparison with captive animals, therefore, can provide baseline information to assess how released horses are adapting to life in Mongolia. The time budget of a Przewalski stallion changed after release from his acclimatisation enclosure in Mongolia (Boyd, 1998). After release he spent less time resting and more time moving than when he was confined, but he still spent a similar amount of time feeding. Initially there is likely to be an exploratory phase

Table 3.2a. Time of day when various behavioural activities occur. If no night figures are given the animals were not observed at that time. Descriptions of activities are given in Chapter 2.

Species	Grazing	Stand resting	Recumbent	Season	Situation	Reference
E. przewalskii	0500-0900 1500-2100	1000-1400	No pattern	Summer	Wild	This study
	0000-1000 1500-0000	0900-1700	0200-0600	Summer	Pre-release	Boyd, 1998
	0400-1100 1600-0000	1100-1900	0200-0600	Summer	Post-release	
	Dusk, dawn	Middle of day			Reserve	Berger *et al.*, 1999
	0800-1200 2000-0400	1200-1600	0000-0400		Captive	Boyd *et al.*, 1988
E.caballus	Dawn-0900 1900-Dusk	0900-1400			Feral	Tyler, 1972
	Dusk, Midnight, Dawn Dawn, day	Middle of day Night		Summer Winter	Feral	Kaseda, 1983b
	Dusk-2200 0400-Dawn	2200-2400 0300-0400	0200-0300		Feral	Keiper *et al.*, 1980
	Early morning Late afternoon	Middle of day				
	More at night More in day			Summer Winter	Feral	Berger, 1986
E. zebra	Dawn-0830 1000-1230 1400-Dusk			Winter	Wild	Penzhorn, 1984
	Dawn-later than 0830 1000-1230 irregularly 1600-Dusk			Summer		
	Dawn-0900 1500-Dusk		0900-1200 1600		Wild	Joubert, 1972

Table 3.2b. Proportion of a day spent in various behavioural activities (see Chapter 2 for descriptions). Figures are percentages or mean percentages (± standard error) of the activity from dawn to dusk (c. 12 hours) or over 24 hours as stated.

Species	Grazing	Stand resting	Standing	Recumbent	Moving	12/24 hours	Season	Situation	Reference
E. przewalskii	52.3	26.4	5.3	1.9	13.6	12	Spring – Autumn	Wild	This study
	47.0	36.4	5.4	3.8	5.3	24	Summer	Pre-release +	Boyd, 1998
	47.8	15.7	7.7	5.3	21.7	24	Summer	Post-release +	
	68.8±8.0	4.0±2.2	14.1±1.4	0	11.9±1.2	12		Small yard *	Boyd, 1988
	44.2±2.8	15.6±1.8	29.5±2.1	0	7.7±0.9	12		Large yard *	
	65.3±6.1	9.6±2.8	19.2±2.5	0.5±0.3	7.5±0.3	12		Pasture *	
	40	30				24	Summer	Reserve	Berger *et al.*, 1999
	62					24	Spring		
	55	48				24	Autumn/ Winter		
	58.4	11.0	3.7	5.5	12.2	24	Summer	Reserve	King, 1996
	46.4±5.9	15.7±3.2	20.6±5.4	5.3±3.5	7.4±1	24		Captive	Boyd *et al.*, 1988
E. caballus	59.5	16.2		7.25	9.48	24	Spring/ Summer	Reserve*	Duncan, 1979
	63.1	21.0		4.3	5.7	24	Autumn/ Winter		
	76.1	19.7				24	Summer	Feral	Kaseda, 1983b
	71.0	27.3				24	Winter		
	Winter> Summer	Summer> Winter				24		Feral	Keiper *et al.*, 1980
	Winter> Summer					12		Feral	Berger, 1986

+ - Time budget of adult stallion only. * - Time budget of adult mares only.

post-release, but if animals continue to move excessively, or do not spend enough time eating sufficient forage, there are risks to their health; body condition may decline and they may reproduce less successfully. Feral horses alter their time budget with the seasons and the same ability in Przewalski horses would show that they could adapt through the year. In addition, studies on the time budget of the animals provides information about their general biology, which is valuable for this species about which almost nothing is known in the wild.

Only one study has previously looked at the synchronicity of activity within a group of horses (van Dierendonck *et al.*, 1996), yet this has many implications for the cohesiveness of a harem. If the harem does not function as a group they will be more vulnerable to predation, and also more likely to disperse. In a small population where there are few conspecifics this could lead Przewalski horses to leave the reserve or join a group of domestic horses and would have a strong impact on the success of the reintroduction.

3.1.2 Vegetation use

The ultimate limit to the number of horses that can be supported in an area is the accessibility of water and the amount of available food. Overgrazing has become a threat in many parts of the world including the rangelands of the American west where feral horses occur, and in Mongolia. It is therefore very important to study what the reintroduced Przewalski horses are eating, in particular if they have a preference for specific vegetation types. It is possible that some skills needed to survive in the wild may have been lost during the thirteen generations that Przewalski horses were in captivity. Life in the wild will be more demanding than in captivity, and the forage will be less nutritious than the feed or grass in zoos or reserves in Europe, so it is important to assess whether they have lost the ability to select vegetation according to their needs.

Research on the diets of feral horses has shown that they are selective feeders and mostly eat grasses (Table 3.3). Feral asses selected more browse and fewer grass species than any population of horses (Woodward & Omhart, 1976). Although the forage species available depends on the study area, many studies feature wheatgrass (*Agropyron* spp.) as a highly selected species. Once their requirements are known, then the availability of preferred foods needs to be studied. The best predictor of habitat used by horses is the abundance of preferred forage plants (Duncan, 1983;

Table 3.3. Vegetation use by different populations of feral horses, and populations of Przewalski horses, mountain zebras and feral asses.

Site	Diet		Reference
	Main species	Plant type	
Western Alberta, Canada	*Carex* spp., *Festuca* spp., *Elymus innovatus*	Grasses and sedge	Salter & Hudson, 1980
Western Alberta, Canada	*Elymus innovatus*, *Festuca* spp.	Grasses, sedges and rushes	Salter & Hudson, 1979
Colorado, USA	*Stipa* spp., *Agropyron* spp., *Bromus* spp.	Grasses	Hansen *et al.*, 1974
Colorado, USA	*Carex* spp., *Agropyron* spp., *Koelaria cristata*, *Bromus* spp.	Grasses and sedges	Hubbard & Hansen, 1976
New Mexico, USA	*Salsola kali*, *Sporobolus* spp., *Prosopsis juliflora*, *Kocleria cristata*, *Agropyron* spp.	Grasses	Hansen, 1976
Wyoming, USA	*Agropyron* spp., *Stipa* spp., *Oyzopsis hymenoides*	Grasses and sedges	Olsen & Hansen, 1977
Wyoming, USA		Sagebush-grassland, saltbush-winterfat	Miller, 1983a
Wyoming, USA	*Stipa* spp., *Agropyron* spp., *Oyzopsis hymenoides*, *Poa* spp.	Grasses, sedges, some browse	Krysl *et al.*, 1984a
Camargue, France	*Juncus* spp., *Scirpus* spp., *Phragmites* spp., *Agropyron* spp., *Brachypodium* spp.	Grasses, reeds	Duncan, 1992
New Forest, UK	*Agrostis* spp., *Molinia caerulea*, other Gramineae	Grasses, browse in winter	Putman *et al.*, 1987
Indian central Himalaya		Forbs, sedges, grasses	Negi *et al.*, 1993
Mongolia – Przewalski horse	*Stipa kylovii*, *Achnatherum splendens*, *Elytrigia repens*	Grasses	Enkhee, 1998
South Africa – Mountain zebra		Grasses	Novellie & Winkler, 1993
	Pentzia incana, *Chrysocoma tenuifolia* – *Eragrostis curvula*	Grasses, dwarf shrubs	Penzhorn, 1982a
California, USA – Feral ass	*Plantago insularis*, *Cercidium floridium*, *Prosopsis* spp.	Forbs and browse	Woodward & Omhart, 1976

Salter & Hudson, 1979). Horses have been shown to maximise intake of high quality food by selecting areas where it has the greatest concentration (Duncan, 1983). Horses change their preferred food species with the seasons. This was shown in America by a change in the food selected in the winter, when there was an increased use of browse and species that were less palatable at other times of year (Hansen, 1976; Krysl *et al.*, 1984a; Krysl *et al.*, 1984b). In the New Forest there also was a change from feeding mostly on grass in the spring, summer and autumn to a diet dominated by browse in the winter (Putman *et al.*, 1987).

It was expected that the Przewalski horses would show a preference for certain vegetation types, in particular to maximise their energy gain; even domestic horses retained this ability despite five thousand years of domestication. There have been only two studies on the food preferences of Przewalski horses released into HNP; both were of relatively short duration and one only covered two harems within acclimatisation enclosures. Both studies found that the horses preferred meadow, mountain steppe and tussock grassland vegetation types (van Dierendonck *et al.*, 1996) or species (*Stipa kylovii, Achnatherum splendens, Elytrigia repens*) (Enkhee, 1998). This study aims to examine the vegetation preferences of the free ranging harems in more detail.

3.2 RESULTS

3.2.1 Home range

The fixed kernel method has been used to estimate range area and use (Worton, 1989) (see Chapter 2, Section 2.4.1 for methods). This results in a different home range size compared to the minimum convex polygon method which has been used in most other studies (Table 3.1). Also, 95% kernel home ranges have been estimated as the home range limits for some analyses to exclude forays that may not be representative of the home range. In all cases, core use areas were 80% of the total range (Appendix III).

100% minimum convex polygon (MCP) estimates of home range size were smaller than 100% kernel home range in eight out of eleven harem-year combinations, but there was no significant difference between the mean MCP and kernel range areas (Table 3.4). Comparisons between results of the two methods are difficult to interpret since they depend partly on the spread of fixes, and must be treated cautiously.

Between 1995 and 2000, 95% kernel home range areas varied in size from 1.3 km^2 to 24.0 km^2 and core use areas (80% kernels) were between 61 ha and 499 ha (Table 3.5). There was no difference in home range size among years ($F_{5, 15} = 0.56$, $p = 0.726$), although it should be noted that the horses were observed for different periods of time within each year. Mean 95% kernel home range areas and 80% use core areas were significantly different among harems (home range: $F_{5, 14} = 6.61$, $p = 0.002$; core area: $F_{5, 14} = 7.65$, $p = 0.001$, both excluding the single home range estimate for Ares). A Tukey's post-hoc test showed that the difference in size of home ranges and core areas was attributable to Patron, whose mean home range and core area was significantly larger than the means of the other harems (Table 3.5).

There was no correlation between the number of fixes and size of the home range (Table 3.5; home range: $r = 0.013$, $p=0.954$; core area: $r = -0.064$, $p=0.783$). In addition, there was no correlation between the size of the home range and number of months since release (Figure 3.1a) or harem size (Figure 3.1b). The relative distribution of the harems' home ranges since release is shown in Figure 3.2.

The population in July 2000 totalled 91 free ranging horses. This gives a density of 0.2 horses km^{-2} over the entire National Park. The average density within a home range since 1995 was 1.8 horses km^{-2} ($n = 24$ home ranges, sd = 1.3 horses km^{-2}) with densities ranging from 5.4 horses km^{-2} (Margad in 2000) to 0.5 horses km^{-2} (Patron in

Table 3.4. Difference in size between two different methods of home range analysis: Minimum Convex Polygon (MCP) and the Kernel method. There was no significant difference between the means of the ranges estimated by the two methods (2-tail paired t = -0.06, df = 19, p = 0.95). One hundred per cent home ranges were used for this analysis.

		Home range estimate		
Harem	Year	MCP	Kernel	Ratio MCP/Kernel
Paritet	1998	1510	1905	0.79
	1999	2890	2176	1.33
	2000	782	1225	0.64
Bayan	1998	1340	459	2.92
	1999	1506	1649	0.91
	2000	781	1003	0.78
Khaan	1998	1097	960	1.14
	1999	1469	1647	0.89
Margad	1999	878	892	0.99
	2000	258	373	0.69
Ares	1998	1069	1104	0.97
Mean		1234	1217	1
CV (%)		54	47	58

Table 3.5. Sizes of home ranges (ha) and harems released in HNP between 1994 and 1998. Home range area = 95% kernels, core areas = 80% kernels. a = Bachelor stallion acquired Khaan's mares. b = Harem was given a hard release from travelling crates near release enclosure 1. There was no difference in mean home range size or mean core area among years, irrespective of harem (home range - $F_{5,15} = 0.56$, p = 726; core area $F_{5,15} = 0.78$, p = 0.578; these include the data for Ares).

Harem	Year	Release enclosure	No. fixes	Period	Home range	Core area	No. adults & juveniles	No. foals	Total harem size
Paritet	1995	1	142	July - December	191	96	7	1	8
	1996		194	January - December	751	275	7	2	9
	1997		131	January - August	881	257	6	3	9
	1998		423	June - October	1233	499	7	4	11
	1999		1166	April - November	1223	408	11	5	16
	2000		586	May - June	709	126	14	2	16
Mean (SD)					832 (387)	277 (156)			
Bayan	1998	1	395	June - October	210	61	6	2	8
	1999		628	April - October	1114	496	8	2	10
	2000		315	May - June	748	320	9	3	12
Mean (SD)					690 (455)	292 (219)			
Margad	1999	a	762	May - October	684	345	14	2	16
	2000		270	May - June	277	126	12	3	15
Mean (SD)					480 (288)	235 (155)			
Khaan	1994	1		NO DATA			6	4	10
	1995		194	April - December	1089	469	9	3	12
	1996		228	January - December	999	367	9	4	13
	1997			NO DATA			13	5	18
	1998		389	June - October	609	249	15	7	22
	1999		199	April - June	1100	523	7	4	11
Mean (SD)					949 (231)	402 (121)			
Ares	1998	2	144	July - October	744	240	6	3	9
Patron	1994	2		NO DATA			6	5	11
	1995		159	April - December	2399	1196	9	3	12
	1996		156	January - December	1904	894	14	4	18
	1997		141	January - July	1653	718	13	2	15
Mean (SD)					1985 (380)	936 (242)			
Turgen	1996	b	96	June - December	751	260	4	1	5
	1997		6	January/April	129	68	3	0	3
Mean (SD)					440 (440)	164 (135)			

Figure 3.1a. Size of the home range and core area of harems since release. There was no correlation between the number of months since release and the core area ($r = -0.01$, $n = 31$, $p = 0.976$), or home range ($r = 0.22$, $n = 31$, $p = 0.235$).

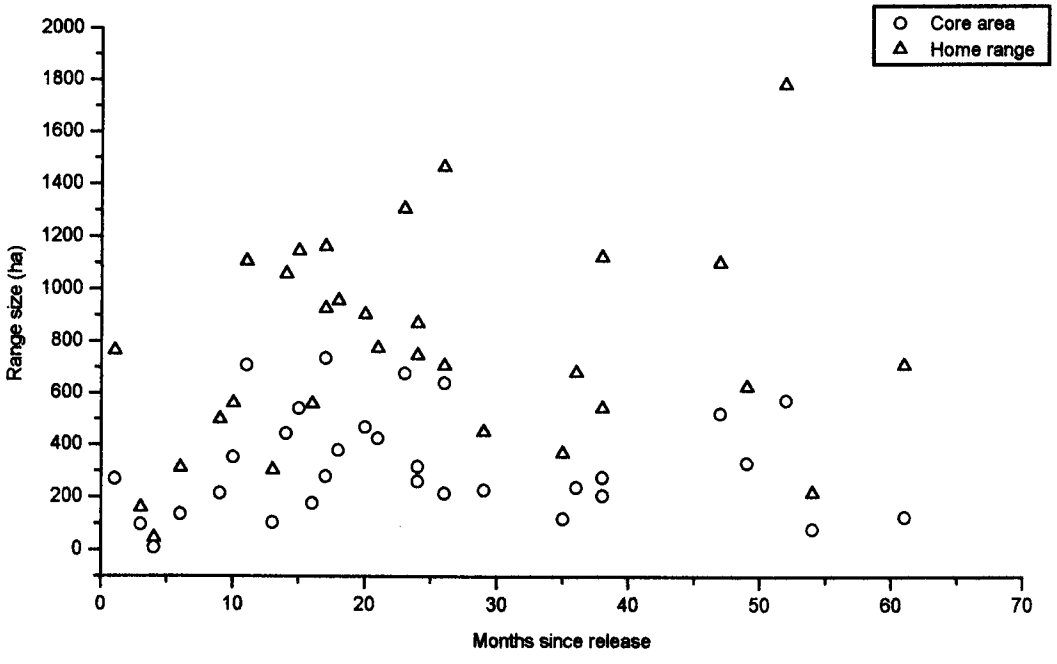


Figure 3.1b. Home range size of harems composed of different numbers of horses. There was no correlation between number of horses and core area ($r = -0.12$, $n = 21$, $p = 0.668$), or home range ($r = 0.29$, $n = 21$, $p = 0.210$).

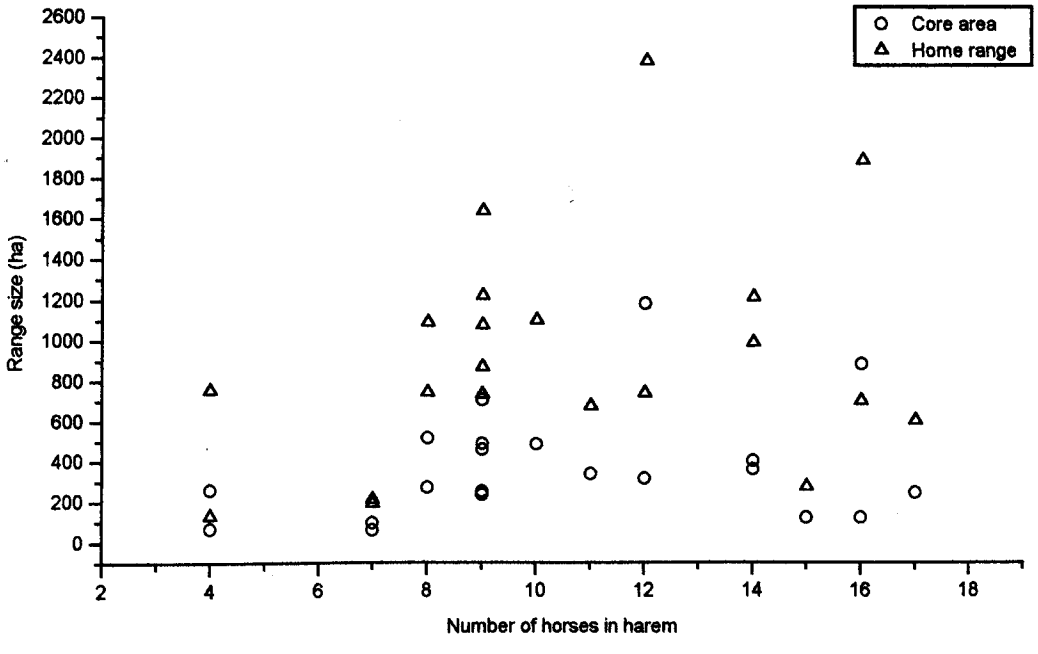
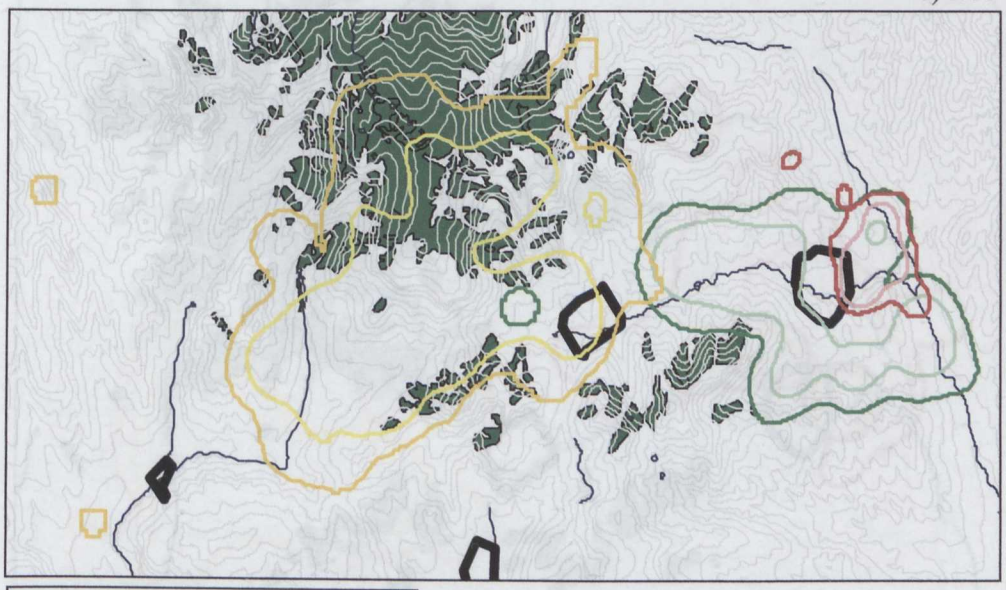
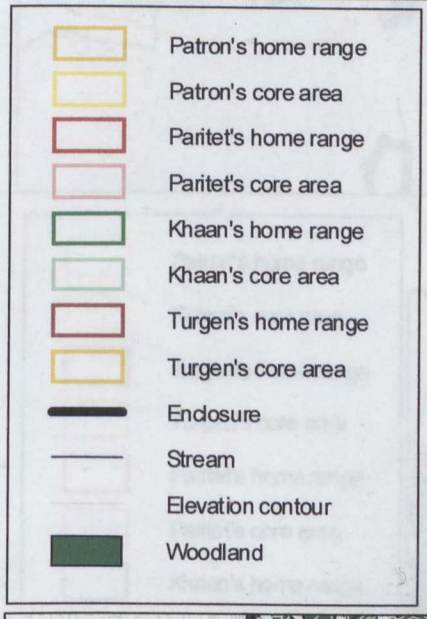
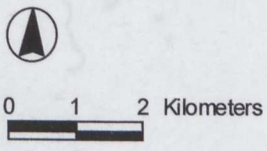


Figure 3.2. Distribution and overlap of home ranges at HNP from 1995 to 2000. Elevation contours are every 25m, from approximately 1250m in the bottom right hand corner of each figure. There are no data for Khaan's harem in 1997.

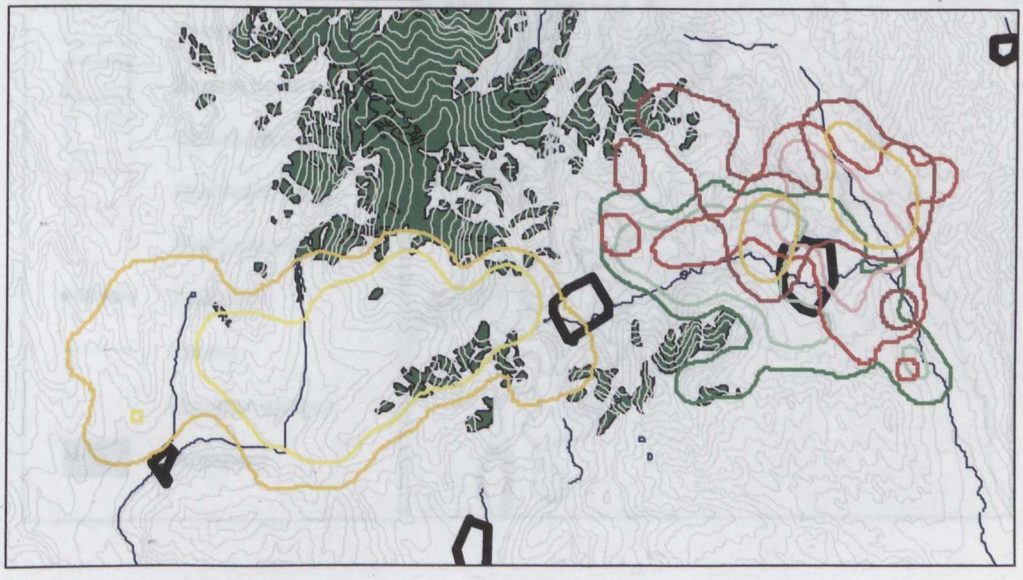
a) 1995

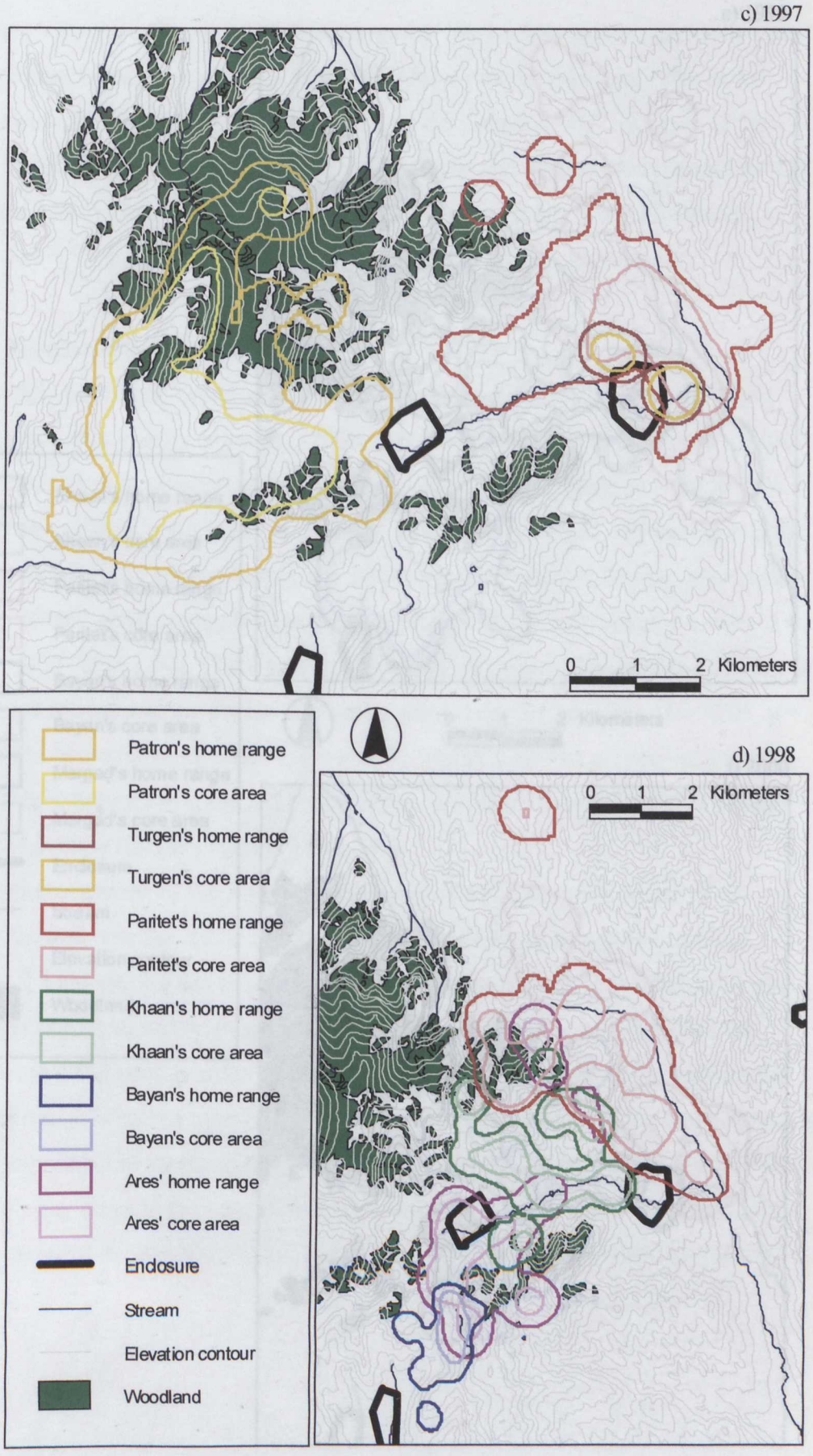




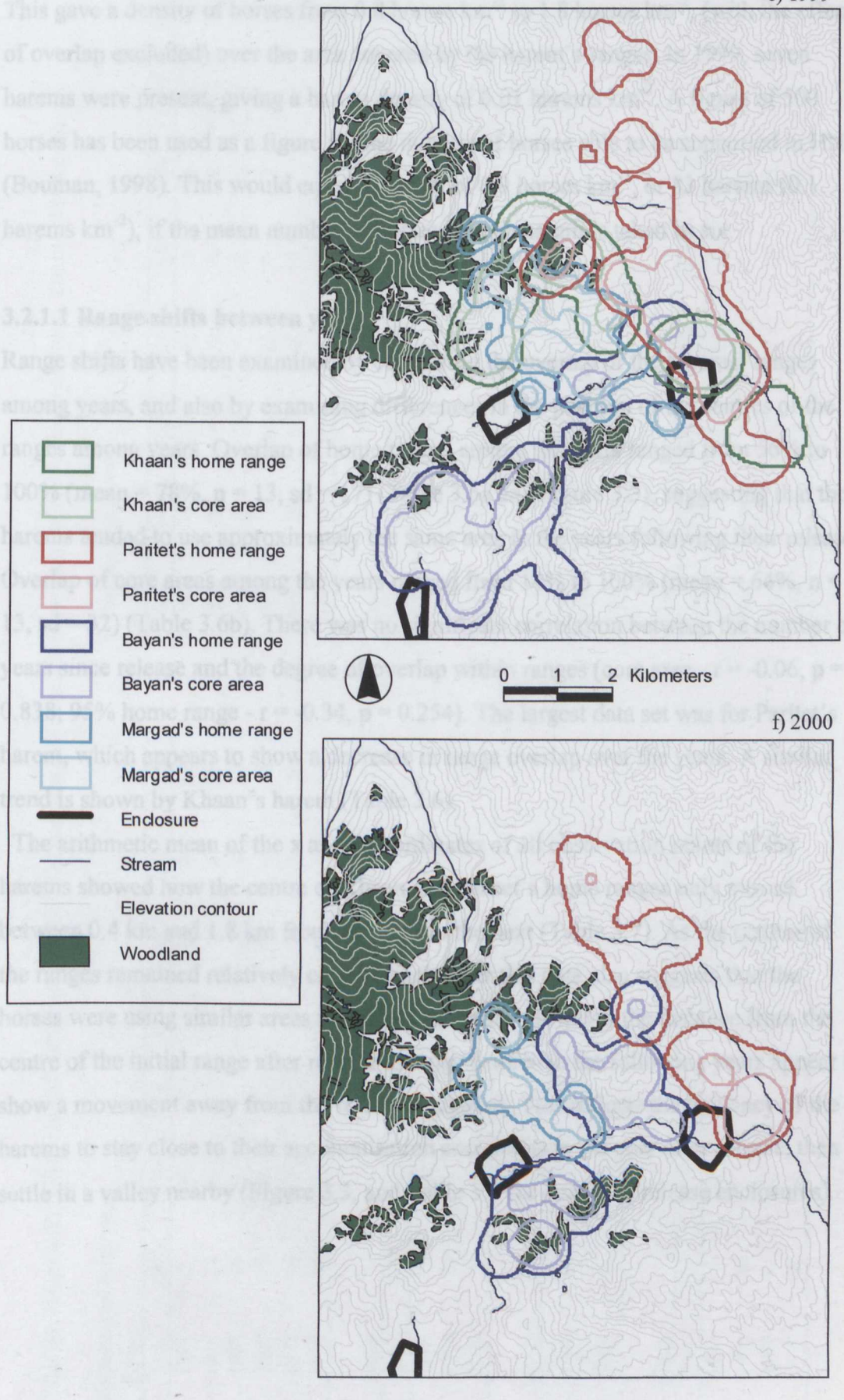


b) 1996




c) 1997
0 1 2 Kilometers
Patron's home range
Patron's core area
Turgen's home range
Turgen's core area
Paritet's home range
Paritet's core area
Khaan's home range
Khaan's core area
Bayan's home range
Bayan's core area
Ares' home range
Ares' core area
Enclosure
Stream
Elevation contour
Woodland
d) 1998
0 1 2 Kilometers

e) 1999


Khaan's home range
Khaan's core area
Paritet's home range
Paritet's core area
Bayan's home range
Bayan's core area
Margad's home range
Margad's core area
Enclosure
Stream
Elevation contour
Woodland
0
1
2 Kilometers

f) 2000

1995). The actual densities per km^2 overall will be higher, due to overlap between the ranges. In 1995, 1996 and 1998 the home range and size of each harem was known. This gave a density of horses from 0.8 horses km^{-2} to 1.8 horses km^{-2}, (with the effects of overlap excluded) over the area covered by the harem's ranges. In 1999, seven harems were present, giving a harem density of 0.01 harems km^{-2}. A figure of 500 horses has been used as a figure for the number of horses able to be supported in HNP (Bouman, 1998). This would equal a density of 0.9 horses km^{-2}, or 83 harems (0.1 harems km^{-2}), if the mean number of horses in each harem is taken as six.

3.2.1.1 Range shifts between years

Range shifts have been examined by comparing the overlap of the harems' ranges among years, and also by examining differences in the position of the centres of the ranges among years. Overlap of home ranges among the years ranged from 56% to 100% (mean = 78%, n = 13, sd = 17) (Table 3.6a and Figure 3.3), suggesting that the harems tended to use approximately the same area in the years following their release. Overlap of core areas among the years ranged from 14% to 100% (mean = 64%, n = 13, sd = 32) (Table 3.6b). There was no significant correlation between the number of years since release and the degree of overlap within ranges (core area - r = -0.06, p = 0.838; 95% home range - r = -0.34, p = 0.254). The largest data set was for Paritet's harem, which appears to show a decrease in range overlap over the years. A similar trend is shown by Khaan's harem (Table 3.6).

The arithmetic mean of the x and y coordinates of all observation points of the harems showed how the centre of Khaan and Paritet's home ranges only moved between 0.4 km and 1.8 km from one year to the next (Table 3.7). As the centres of the ranges remained relatively close to each other this data also suggests that the horses were using similar areas in subsequent years. However the distance from the centre of the initial range after release to range centres in the following years appear to show a movement away from the release enclosure. This reflects the tendency of the harems to stay close to their acclimatisation enclosures in the year after release, then settle in a valley nearby (Figure 3.3, and Table 3.5 for details of release enclosures).

Table 3.6. Range shifts of home ranges and core areas within a harems range expressed as a percentage of the overlap in each year. Columns overlap rows.

a) Overlap of home range

Paritet

Year	1995	1996	1997	1998	1999	2000	Total
1995	*	100	93	75	89	87	100
1996	25	*	75	47	60	41	85
1997	20	64	*	62	64	45	86
1998	12	28	44	*	62	44	73
1999	14	37	46	62	*	37	74
2000	24	44	56	76	65	*	82

Bayan

Year	1998	1999	2000	Total
1998	*	98	18	98
1999	19	*	33	48
2000	5	49	*	49

Margad

Year	1999	2000
1999	*	31
2000	76	*

Khaan

Year	1995	1996	1998	1999	Total
1995	*	78	23	36	85
1996	85	*	31	34	92
1998	41	50	*	41	84
1999	36	31	23	*	56

b) Overlap of core area

Paritet

Year	1995	1996	1997	1998	1999	2000	Total
1995	*	100	82	24	86	89	100
1996	35	*	79	39	78	45	96
1997	31	79	*	48	76	44	94
1998	5	42	25	*	47	9	48
1999	20	52	48	57	*	25	86
2000	68	97	90	35	82	*	98

Bayan

Year	1998	1999	2000	Total
1998	*	51	0	51
1999	6	*	11	18
2000	0	18	*	18

Margad

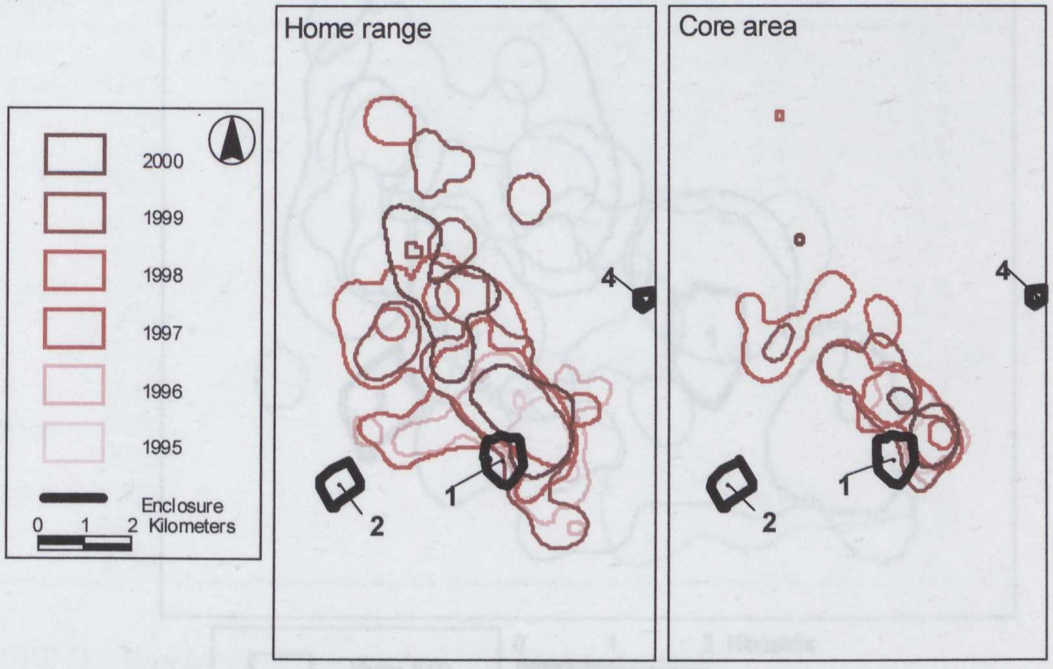
Year	1999	2000
1999	*	20
2000	54	*

Khaan

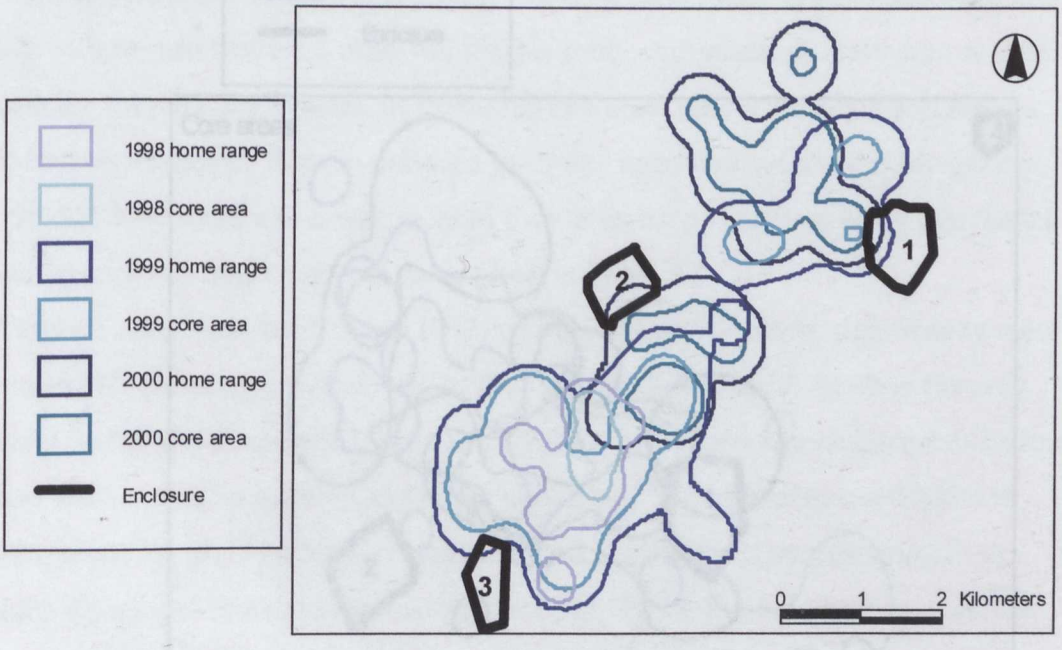
Year	1995	1996	1998	1999	Total
1995	*	61	23	4	61
1996	78	*	34	7	86
1998	43	50	*	19	68
1999	4	0	9	*	14

Figure 3.3. Overlap within home ranges 1995 - 2000. There are no data for Khaan's harem in 1997.

a) Paritet's harem



b) Bayan's harem



c) Khaan and Margad's harems

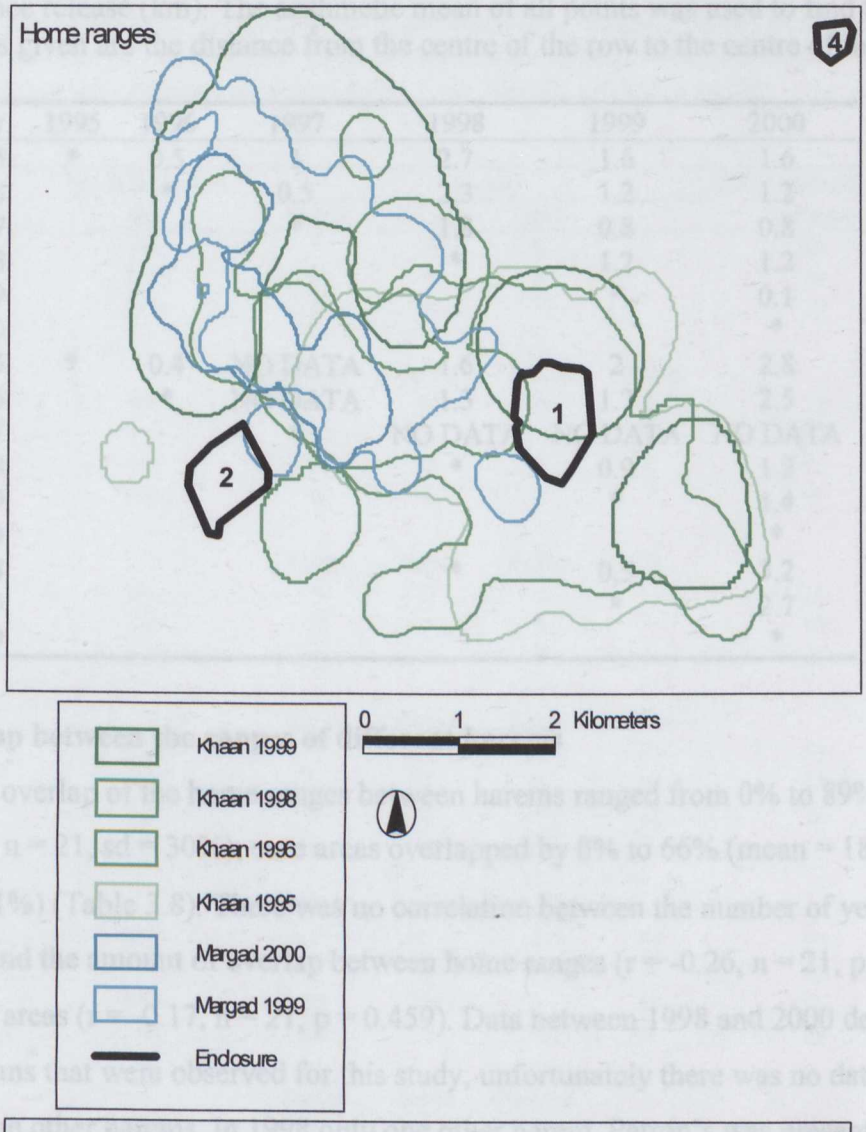


Table 3.7. Distance from the centre of the home range in one year to the centre in all other years since release (km). The arithmetic mean of all points was used to find the centre. Figures given are the distance from the centre of the row to the centre of the column.

Harem	Year	1995	1996	1997	1998	1999	2000
Paritet	1995	*	0.5	1	2.7	1.6	1.6
	1996		*	0.5	2.3	1.2	1.2
	1997			*	1.8	0.8	0.8
	1998				*	1.2	1.2
	1999					*	0.1
	2000						*
Khaan	1995	*	0.4	NO DATA	1.6	2	2.8
	1996		*	NO DATA	1.3	1.7	2.5
	1997			*	NO DATA	NO DATA	NO DATA
	1998				*	0.9	1.2
Margad	1999					*	1.4
	2000						*
Bayan	1998				*	0.5	3.2
	1999					*	2.7
	2000						*

3.2.1.2 Overlap between the ranges of different harems

The degree of overlap of the home ranges between harems ranged from 0% to 89% (mean = 39%, n = 21, sd = 30%); core areas overlapped by 0% to 66% (mean = 18%, n = 21, sd = 21%) (Table 3.8). There was no correlation between the number of years since release and the amount of overlap between home ranges ($r = -0.26$, $n = 21$, $p = 0.253$) or core areas ($r = -0.17$, $n = 21$, $p = 0.459$). Data between 1998 and 2000 dealt only with harems that were observed for this study; unfortunately there was no data available for the other harems. In 1998 only one other harem, Patron's was present. No harem overlapped them in previous years and none was observed subsequently. In 1999 and 2000 there was a maximum of four other harems, so it is likely that the total overlap area was larger than the value given in Table 3.8.

Turgen's core area (in 1996 and 1997) was overlapped by others significantly more than any other harem except Ares' (in 1998) (Table 3.8b). In 1995 (when Paritet's harem was first released and Khaan's and Patron's had been free ranging for one year) there was no overlap between any of the core areas. The core areas overlapped in 1996, when Turgen's harem was released in the same area as the enclosure from which Khaan and Paritet had been released (Figure 3.2). Patron's core area did not overlap with any other harem between 1995 and 1997, and did not appear to do so subsequently (pers. obs). The bachelor group moved among the home ranges of all harems and so overlapped with them all (pers. obs.).

Table 3.8. Overlap of home ranges and core areas between harems expressed as a percentage of the area covered in each year. Columns overlap rows. There was no difference among the harems in the overlap of home ranges ($F_{6, 14} = 1.66$, $p = 0.204$), but there was a difference among the overlap of core areas ($F_{6, 14} = 3.53$, $p = 0.024$).

a) Home range

Year	Harem	Home range area (ha)	Harem				Total % of range area overlapped
			Paritet	Khaan	Patron		
1995	Paritet	191	*	86	0		86
	Khaan	1089	15	*	4		19
	Patron	2399	0	39	*		39
1996			Khaan	Paritet	Turgen	Patron	
	Khaan	999	*	42	25	0	51
	Paritet	751	56	*	53	0	87
	Turgen	751	34	53	*	0	85
	Patron	1904	0	0	0	*	0
1997			Paritet	Turgen	Patron		
	Paritet	881	*	13	0		13
	Turgen	129	89	*	0		89
	Patron	1653	0	0	*		0
1998			Khaan	Paritet	Bayan	Ares	
	Khaan	609	*	14	0	29	35
	Paritet	1233	7	*	0	12	14
	Bayan	210	0	0	*	41	41
	Ares	744	24	19	12	*	18
1999			Paritet	Bayan	Margad	Khaan	
	Paritet	1223	*	8	6	37	40
	Bayan	1114	9	*	11	9	23
	Margad	684	10	19	*	49	66
	Khaan	1100	41	9	30	*	68
2000			Paritet	Bayan	Margad		
	Paritet	709	*	8	0		8
	Bayan	748	8	*	5		13
	Margad	277	0	14	*		14

b) Core area

Year	Harem	Core range area (ha)	Harem				Total % of core area overlapped
			Paritet	Khaan	Patron		
1995	Paritet	96	*	0	0		0
	Khaan	469	0	*	0		0
	Patron	1196	0	0	*		0
1996			Khaan	Paritet	Turgen	Patron	
	Khaan	367	*	5	20	0	21
	Paritet	275	7	*	34	0	35
	Turgen	260	29	36	*	0	66
	Patron	894	0	0	0	*	0
1997			Paritet	Turgen	Patron		
	Paritet	257	*	16	0		16
	Turgen	68	59	*	0		59
	Patron	718	0	0	*		0
1998			Khaan	Paritet	Bayan	Ares	
	Khaan	249	*	4	0	0	5
	Paritet	499	2	*	0	3	5
	Bayan	61	0	0	*	33	33
	Ares	240	0	5	8	*	14
1999			Paritet	Bayan	Margad	Khaan	
	Paritet	408	*	5	0	31	35
	Bayan	496	4	*	5	1	9
	Margad	345	0	7	*	23	32
	Khaan	523	0	1	15	*	39
2000			Paritet	Bayan	Margad		
	Paritet	126	*	0	0		0
	Bayan	320	0	*	1		1
	Margad	126	0	1	*		1

A reduction in overlap among core areas of some harems reflects range shifts and/or a change in area (Figures 3.2 and 3.3). For instance Bayan's harem only overlaps with Ares' in 1998, but in 1999 overlaps with all other harems as he uses a larger area. It is also interesting to note the overlap between Khaan and Margad's harems (Figures 3.2e and 3.3c). In 1999 the bachelor stallion Margad took most of Khaan's mares, and although they were using the same valley, their core areas only overlapped by 23%, suggesting they avoided each other. At the end of June, Khaan's remaining mares were taken by another stallion and moved to a different valley. It then appeared that Margad's harem used increasingly more of Khaan's previous range; in 2000, 50% of Margad's core area (78% of the home range) overlapped with Khaan's 1998 core area and 57% with Khaan's 1999 core area.

Although the harems appeared to avoid each other there was no evidence of exclusive use of an area by any harem. The harems appeared to select a home range in a valley where there were no previous horses, and where the harems were separated by ridges. There is thus possible evidence that harems separate themselves, possibly to minimise losses of mares. However Bayan broke the trend by tending to use the same valley as Margad in 2000, and observations have been made of all harems in the same valley during the winter (pers. comm. Mongolian rangers).

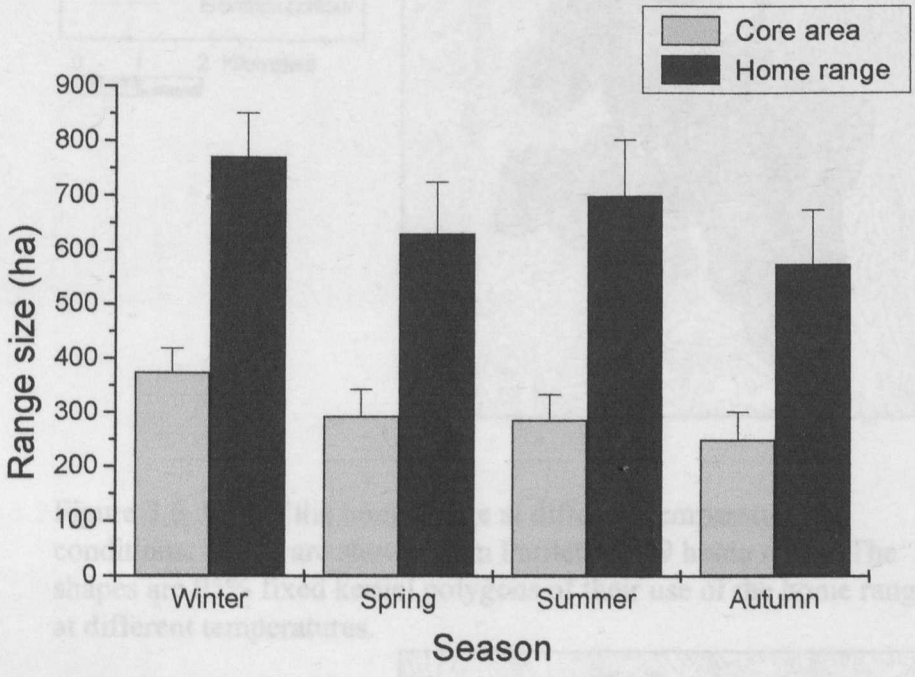
3.2.1.3 Use of the home range

Home range use is influenced by several factors including temperature, season, time of day and flies. There was no significant difference in the size of the ranges in the different seasons, although there was a tendency for them to be slightly larger in the winter (Figure 3.4).

In their core areas, the horses tended to be found at a higher altitude during the summer than in spring or autumn (median in summer = 1500 m, spring = 1425 m and autumn = 1400 m) ($H = 613.31$, $df = 2$, $p = <0.0001$; see Figure 3.5, using Paritet's harem as an example). In the summer the horses would spend the night in the valleys, moving up to the ridges for the heat of the day. In the spring and autumn this movement was not so marked as the horses spent more time at lower elevations. This is reflected in the movement of the horses between successive sample points. The horses moved significantly less in the spring (mean = 70 m, median = 9 m, IQR = 4 - 96 m, n = 1046) than in autumn (mean = 97 m, median = 12 m, IQR = 6 – 132 m, n = 2649) and summer (mean = 81 m, median = 13 m, IQR = 7 – 121 m, n=1288)

(H=57.99, df=2, p=<0.0001). Although the distribution of these data is very skewed the general pattern is clear. When moving, the horses occasionally covered large distances - Khaan's harem was observed to move over 2.5km between successive ten minute sample points in the summer of 1999.

Figure 3.4. Mean size of home ranges (1995 – 2000) in the different seasons (+ 1se). There was no significant difference in the size of the core areas among seasons ($F_{3,39} = 0.62$, $p = 0.605$), or home ranges ($F_{3,39} = 0.49$, $p = 0.693$).



There was a difference in the activity of horses according to elevation (H = 626.76, df = 6, p = <0.0001). The horses tended to graze more at lower elevations (median = 1400m) and stand rest higher up (median = 1500m). There was a positive correlation between temperature and elevations where the horses were found ($r_s = 0.54$, p = <0.0001). In cooler weather they were found in the valleys, but as it got hotter they were found more frequently at high elevations (Figure 3.6, using Paritet's harem in 1999 as an example). The areas used by the horses to rest and shelter from the flies were normally among trees or at rocky outcrops near ridges (Plates 3.1 and 3.2). However one harem, Bayan's, used a small patch of forest in a gully in 1998. The horses also used different elevations at different times of day (H = 759.16, df = 23, p =

Figure 3.5. Seasonal use of the home range. Observation points of Paritet's harem in 1996, 1997 and 1999 are shown. The shapes are 95% fixed kernel polygons of home range use in each season in those years. Points and shapes from 1995, 1998 and 2000 are not shown as only two seasons were observed in those years.

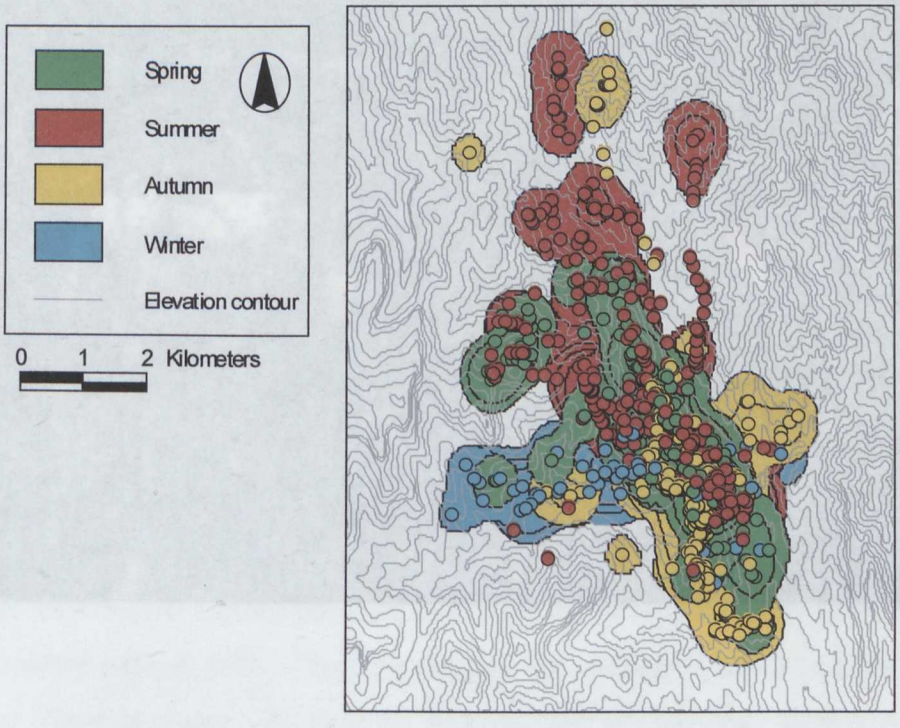


Figure 3.6. Use of the home range at different temperature conditions. Points are shown from Paritet's 1999 home range. The shapes are 95% fixed kernel polygons of their use of the home range at different temperatures.

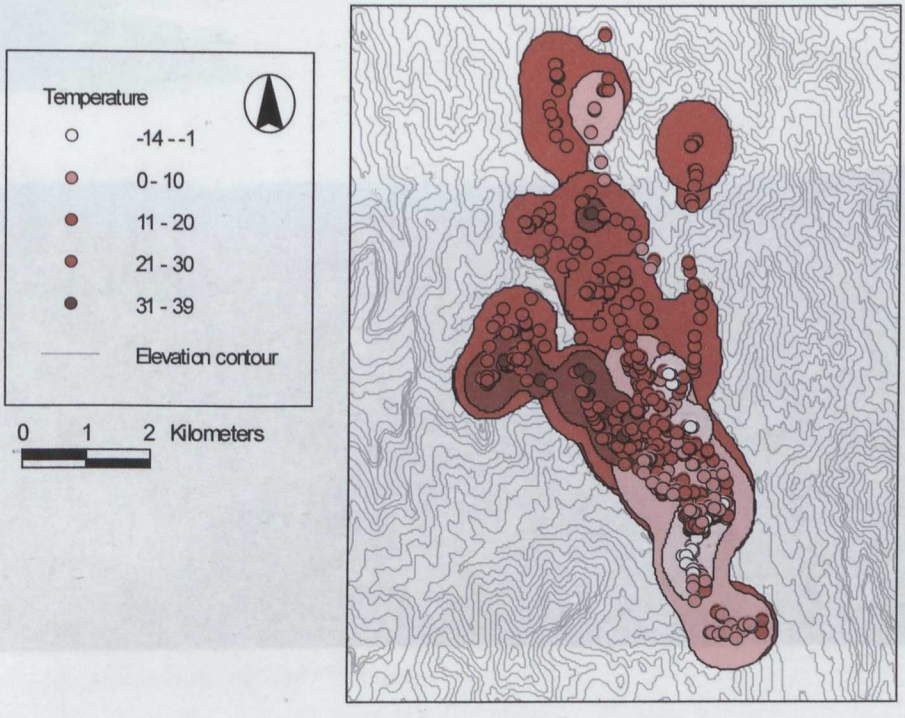


Plate 3.1. Resting among trees.

Plate 3.2. Resting by rocks.

<0.0001). Between 1000h and 1500h the median elevation of the horses was 1500 m, but at 0400h and 2200h the median was 1300 m.

Thus the horses spent the morning grazing, moving through the valleys, then moved up to ridges to stand rest in one place through the heat in the middle of the day. This pattern was less marked in the spring and autumn when the weather was cooler and the horses spent more time at lower elevations.

Harems tended to have different elevation ranges ($H = 725.40$, $df = 3$, $p = <0.0001$). Overall, Paritet was found more often at a lower elevation (median = 1375 m), whereas Bayan was found higher (median = 1500 m). However, this is more likely to reflect the location of the home range than a preference for or against altitude.

All home ranges contained a year round water source, an area of rocky outcrops near a ridge, and patches of forest, which were used in the summer. Ares', Bayan, Khaan and Margad's harems all overlapped at a particular place along the stream where pools were formed and the banks had been eroded to form a salt lick. The majority of encounters between the harems occurred here (pers. obs.). The home ranges seemed to occupy separate valleys, defined by their ridges which peaked at about 1600 m, but which also joined at passes and along the watercourses. Within these valleys there were countless gullies and smaller ridges that were exploited by the horses for their shelter and forage.

3.2.2 Time budget

3.2.2.1 Effect of time

Grazing and stand-resting were the most common behaviours, together taking up nearly three-quarters of the horses' time budget. Lying down and standing were relatively rare behaviours; lying down was not observed in every harem in every year. The time budget of the harems is summarised in Tables 3.9a and 3.9b, and shown in Figures 3.7 and 3.8. As the pattern of behaviours through the day was similar among the harems (see below), data pooled from all harems and all years is shown graphically. For grazing and stand resting the harems all appear to follow the same general trend, but the pattern of behaviour use was less clear in the less frequent activities both within and between harems.

Drinking was not analysed, but appeared to take place in the morning and evenings during the summer, when the horses came down from the ridges to graze (pers. obs). In the cooler months when the horses remained close to water, no pattern was noticed.

Table 3.9a. Daily time budgets of each harem (% time spent in each activity). Figures in brackets indicate time budget from 2100h to 0450h.

Activity	Paritet			Bayan			Khaan		Margad		Ares
	1998	1999	2000	1998	1999	2000	1998	1999	1999	2000	1998
Grazing	46	55	55 (59)	42	53	39	54	62	56	62	39
Recumbent	0	1	6 (22)	0	1	0	2	0	1	1	1
Moving	21	13	14 (9)	12	14	12	18	12	13	8	14
Standing	4	4	3 (3)	5	5	6	3	10	9	1	9
Stand resting	28	27	22 (6)	41	25	43	23	16	20	27	38

Table 3.9b. Daily time budgets of each harem pooled over the years they were observed.

Activity	Paritet	Bayan	Khaan	Margad	Ares
Grazing	53	47	56	58	39
Recumbent	2	0	1	1	1
Moving	14	13	16	12	14
Standing	4	5	5	7	9
Stand resting	26	34	21	22	38

3.2.2.1a Grazing

All harems grazed more at certain times of the day in every year they were observed (Appendix IV). There tended to be bouts of grazing in the early morning (between 0500h and 0900h) and in the afternoon/evening (between 1500h and 2100h), although this varied slightly among harems and years. The time of year also affected how much time the horses spent grazing and when it occurred, as the horses tended to graze through more of the day in the cooler months (Friedman's $F = 46878$, $df = 2$, $p = <0.0001$). All harems grazed significantly more in the spring and autumn than in the summer ($H = 210.03$, $df = 2$, $p = <0.0001$). The temperature and the emergence of flies, as well as the growing cycle of the vegetation, is related to the time of year, and it is unclear which of these factors affect the horses' grazing times more.

Only Paritet's and Bayan's harems showed a difference in the amount of time they spent grazing among the years. Paritet's harem spent more time grazing in 1998 and Bayan's harem grazed more in 1999 (Appendix IV). There was a difference in the

Figure 3.7. Hourly time budget of all harems pooled over all years.
Data between 2200 and 0400 is from Paritet's harem in 2000.

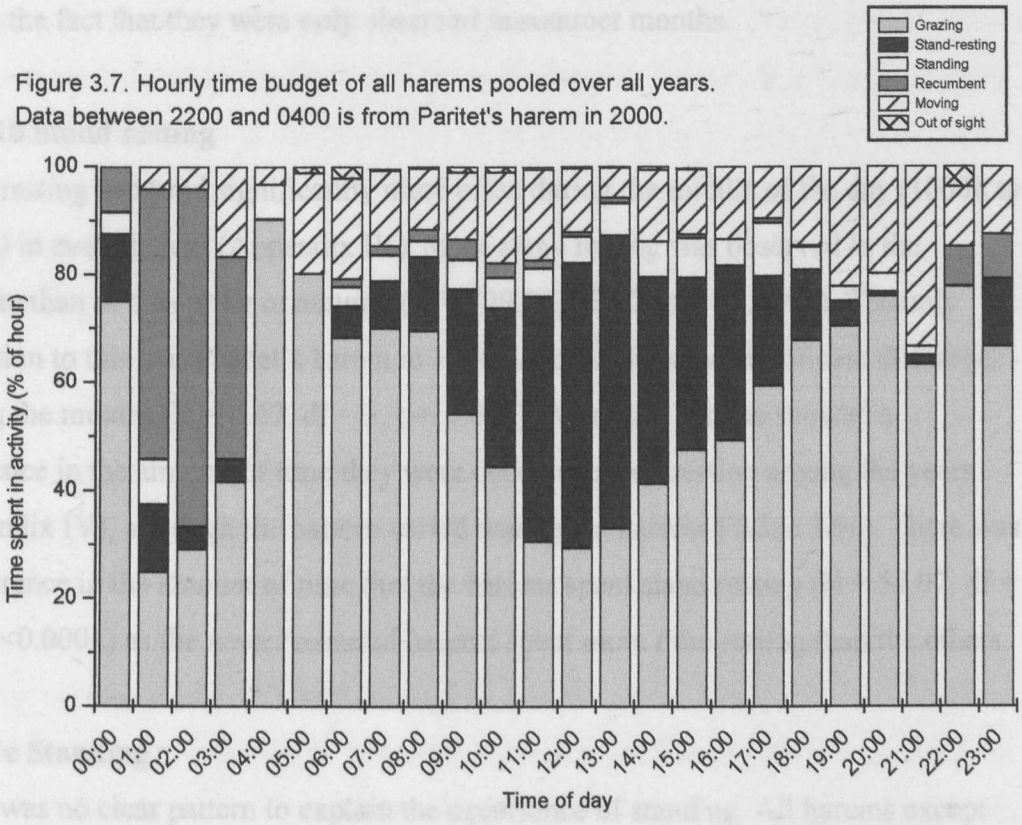
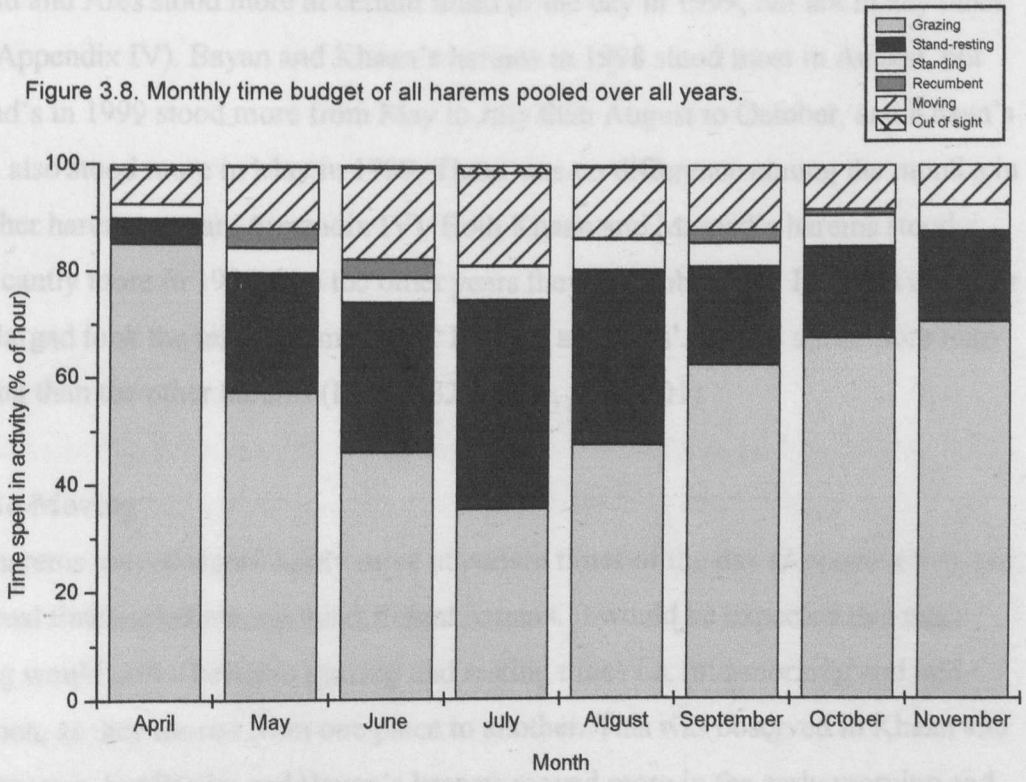


Figure 3.8. Monthly time budget of all harems pooled over all years.



amount of time that the harems spent grazing (H = 54.07, df = 4, p = <0.0001; Table 3.9b). The relatively small amount of time Ares' harem spent grazing is likely to be due to the fact that they were only observed in summer months.

3.2.2.1b Stand resting

Stand resting occurred significantly more often during the middle of the day (1000h to 1400h) in every harem (Appendix IV). More stand resting was observed in the summer than in the spring or autumn (H = 129.88, df = 2, p = <0.0001). The only exception to this was Paritet's harem in 1998 which showed no significant difference among the months (H = 6.67, df = 3, p = 0.083). All of the harems showed a difference in the amount of time they were observed stand resting among the years (Appendix IV), although the pattern varied among the harems (Table 3.9a). There was a difference in the amount of time that the harems spent stand resting (H = 54.07, df = 4, p = <0.0001) as the newer released harems spent more time resting than the others.

3.2.2.1c Standing

There was no clear pattern to explain the occurrence of standing. All harems except Margad and Ares stood more at certain times of the day in 1999, but not in any other year (Appendix IV). Bayan and Khaan's harems in 1998 stood most in August, but Margad's in 1999 stood more from May to July than August to October, and Khaan's harem also stood more in May in 1999. There was no difference among the months in any other harem or year (Appendix IV). Both Khaan and Margad's harems stood significantly more in 1999 than the other years they were observed. It was in this year that Margad took the mares from Khaan. Margad and Ares' harems spent more time standing than the other harems (H = 18.82, df = 4, p = 0.001).

3.2.2.1d Moving

Most harems moved significantly more at certain times of the day (Appendix IV), but the actual time varied among the different harems. It would be expected that most moving would occur between grazing and resting times i.e. mid-morning and mid-afternoon, as they moved from one place to another. This was observed in Khaan and Ares' harems, but Paritet and Bayan's harems moved more in the early morning and late evening. Margad's harem did not move more at specific times in any year, and Bayan's showed no significance in 1998. All harems moved more in certain months of

the year, particularly the autumn. For example, in autumn 1999 Paritet's harem moved more than 10km from their core area and back again in the same day. The frequency of moving varied among the years in all harems except Bayan's. Paritet's and Khaan's harems moved significantly more in 1998, and Margad's harem moved more in 1999. There was no difference in the time spent moving among the harems ($H = 6.92$, $df = 4$, $p = 0.140$).

3.2.2.1e Recumbent rest

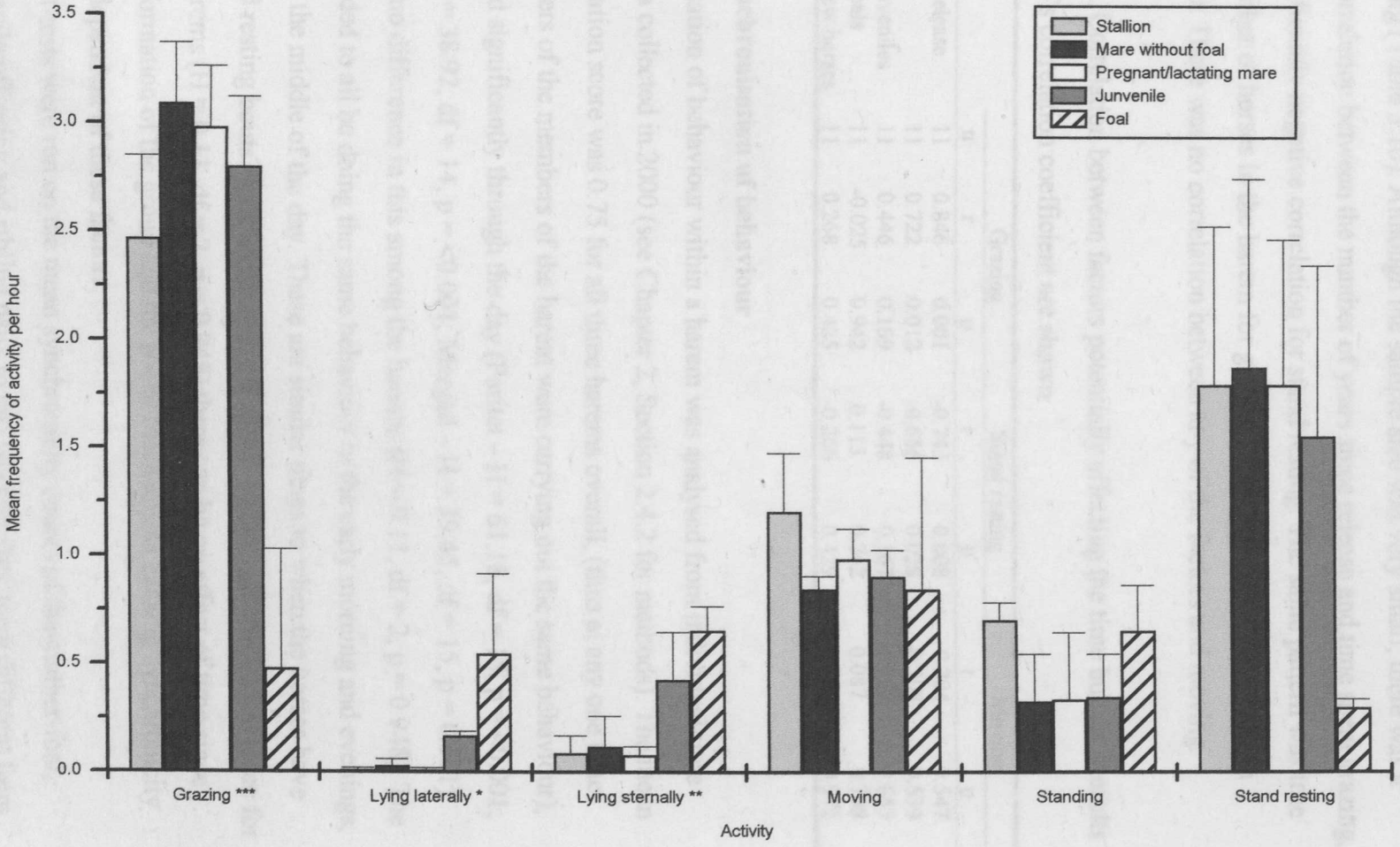
This behaviour was not observed among the whole of Paritet and Bayan's harems in 1998, Khaan's harem in 1999 or Bayan's harem in 2000, and in all other cases it was very rare during the day (Table 3.9a). In 2000 Paritet's harem were observed over 24 hours, and lying down made up 11% of its time budget. Sixty five per cent ($n = 65$) of observations of the harem lying down in 2000 were at night, with 55% of all recumbency occurring between 0100h and 0300h, a time when most recumbent rest was seen in other studies (Table 3.2a).

In 1999 both Bayan and Margad's harems showed a significant difference among the hours when they lay down (Bayan's harem were observed in recumbent rest at 0800h, and Margad's harem from 0900h to 1000h and at 1300h). In 1999 all harems also showed a difference among the months, and this was true for Khaan in 1998 (recumbent rest was observed in June) (Appendix IV). Post hoc tests did not show where any differences lay, however as this behaviour was rare, in some cases it was only observed in one month, or hour. The significance is more likely to reflect this, rather then a trend for lying down at certain times.

3.2.2.2 Effect of age and sex

The individual time budget data collected in 2000 were used to find the effect of age and sex and lactation and/or pregnancy on the frequency of each behaviour. The mean frequencies of each behaviour observed in each age and sex class were analysed using a two-way ANOVA to assess differences among them. For all behaviours except grazing, lying laterally and lying sternally there were no differences among ages and sexes (Figure 3.9). Foals grazed significantly less than any other age or sex group. Foals also lay laterally and sternally significantly more than other age and sex classes, except for juveniles. Juveniles lay sternally significantly more frequently than lactating mares.

Figure 3.9. Differences in the mean frequency of activity of the different ages and sexes of Paritet, Bayan and Margad's harems, 2000 (+ 1 sd).
ANOVA: *** = p<0.0001, ** = p0.001, * = p<0.05



3.2.2.3 Effect of other factors on time budget

Factors such as the number of new horses, the number of juveniles, the number of horses in the harem, the number of foals and the number of years since release were examined to see if they were associated with the frequency of grazing, moving and stand-resting (Table 3.10). Although the sample size was very small, there was a positive correlation between the number of years since release and time spent grazing, and a significantly negative correlation for stand resting. The same pattern was true for the number of horses in the harem for grazing and stand resting, as shown in Figure 3.10. There was no correlation between any of the factors and moving.

Table 3.10. Correlation between factors potentially affecting the time budget. Results of Pearson's correlation coefficient are shown.

Factor		Grazing		Stand resting		Moving	
	n	r	p	r	p	r	p
Years since release	11	0.846	0.001	-0.745	0.008	-0.204	0.547
Harem size	11	0.722	0.012	-0.656	0.028	-0.208	0.539
Number of juveniles	11	0.446	0.169	-0.448	0.167	-0.152	0.655
Number of foals	11	-0.025	0.942	0.113	0.742	0.087	0.798
Number of new horses	11	0.268	0.425	-0.266	0.429	-0.012	0.972

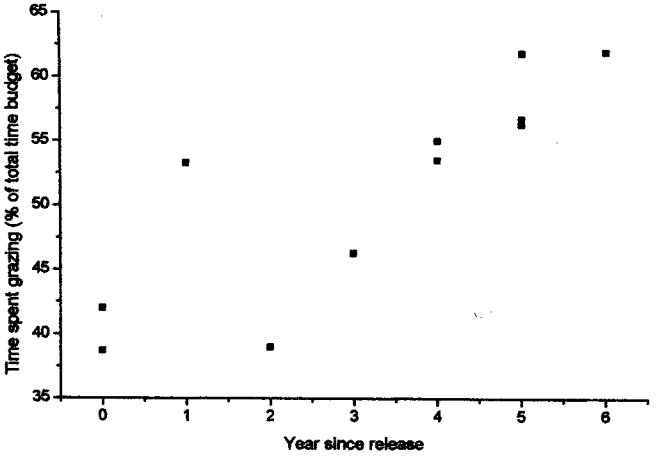
3.2.2.4 Synchronisation of behaviour

Synchronisation of behaviour within a harem was analysed from individual time budget data collected in 2000 (see Chapter 2, Section 2.4.2 for methods). The mean synchronisation score was 0.75 for all three harems overall, (thus at any one time three-quarters of the members of the harem were carrying out the same behaviour), but it varied significantly through the day (Paritet – $H = 61.18$, $df = 15$, $p = <0.001$; Bayan – $H = 38.92$, $df = 14$, $p = <0.001$; Margad – $H = 39.45$, $df = 15$, $p = 0.001$). There was no difference in this among the harems ($H = 0.11$, $df = 2$, $p = 0.948$). The harems tended to all be doing the same behaviour in the early morning and evenings, and also in the middle of the day. These are similar times to when the horses have grazing and resting bouts. As there was no difference in the synchronisation score for all three harems ($H = 0.11$, $df = 2$, $p = 0.948$) there can be no effect of time since release or formation of the group and the social mechanisms causing synchronicity must be independent of these factors.

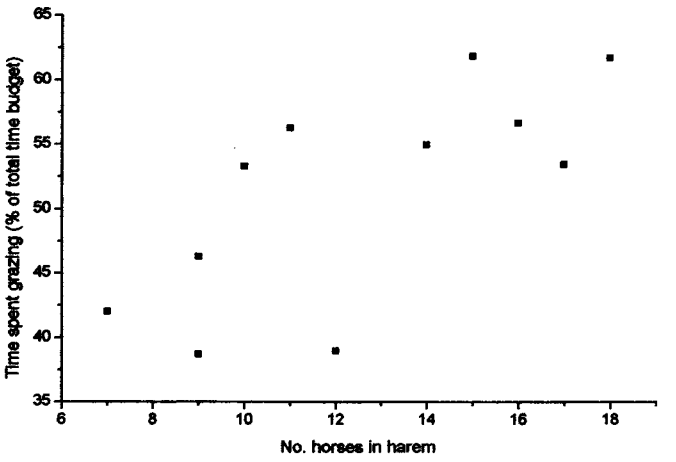
Unpaired t-tests were run on the mean synchronicity counts of the mother-foal, mother-juvenile offspring and sibling pairs to test whether they were different from the mean synchronicity within the harem. Mother – foal dyads were less synchronous

Figure 3.10. Effect of number of horses in the harem and time since release on grazing and stand resting behaviour.

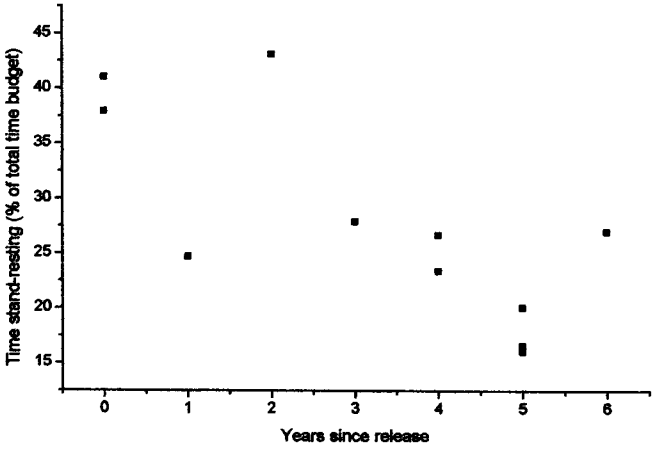
a) r = 0.85, p = 0.001



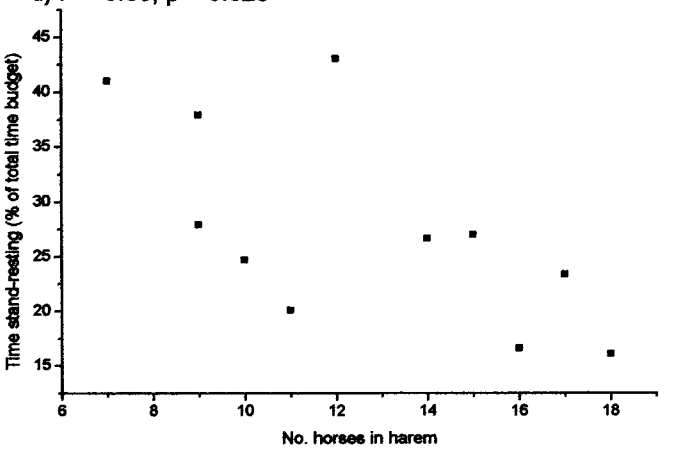
b) r = 0.72, p = 0.012



c) r = -0.75, p = 0.008



d) r = -0.66, p = 0.028



than the harem as a whole (T = -4.06, df = 5, p = 0.0097), but mother – juvenile dyads were more synchronous (T = 5.18, df = 12, p = 0.0002). There was no difference between the synchronicity of sibling pairs and the harem as a whole (T = 0.91, df = 2, p = 0.46), however the sample size was very small. A percentage value of the amount of time each pair of animals were doing the same behaviour is shown in Appendix V. Whether the rest of the harem tended to be exhibiting the same behaviour as the stallion was found to be not significantly different from synchronicity within the harem as a whole (T = -1.26, df = 2, p = 0.33). Interestingly, Bayan had a greater synchronicity with the rest of his harem than the other two stallions (Appendix V).

3.2.3 Vegetation use

The horses were observed grazing on all eleven vegetation classes described by Wallis de Vries *et al.* (1996) (Table 3.11). The different home ranges were composed of slightly different vegetation classes reflecting their different terrain and aspect (Figure 3.11).

The selection index of the different vegetation classes for grazing by each harem in each year is shown in Table 3.12 (full details of vegetation class selection indices and calculations are in Appendix VI). Every harem used some vegetation classes more than would be expected if they were randomly using a vegetation class in proportion to its availability (Appendix VII). Vegetation classes selected varied among the harems and years. This was particularly shown by Bayan's harem, who only grazed on six of the ten vegetation classes covered by their 1998 home range, and of that six, only three vegetation classes had a sample count of more than five. In 1998 the horses used fewer vegetation classes than in the other years. The harems seemed to change their preferences over the years with the exception of Bayan's harem, which selected Mountain steppe II in both 1998 and 1999, and Margad's, which selected this vegetation class in 1999 and 2000.

The horses most frequently selected vegetation classes from the lower elevations (Meadow I, Tussock grassland and Lowland steppe). Meadow I had the highest selection index by Bayan's harem in 1999 and 2000. It also had a very high selection index of 12.44 by Khaan's harem in 1998 and was selected more than any other vegetation class, however it was not used in 1999 by Khaan's harem, or by Margad's harem (except for marginal significance in 2000). Meadow I is dominated by

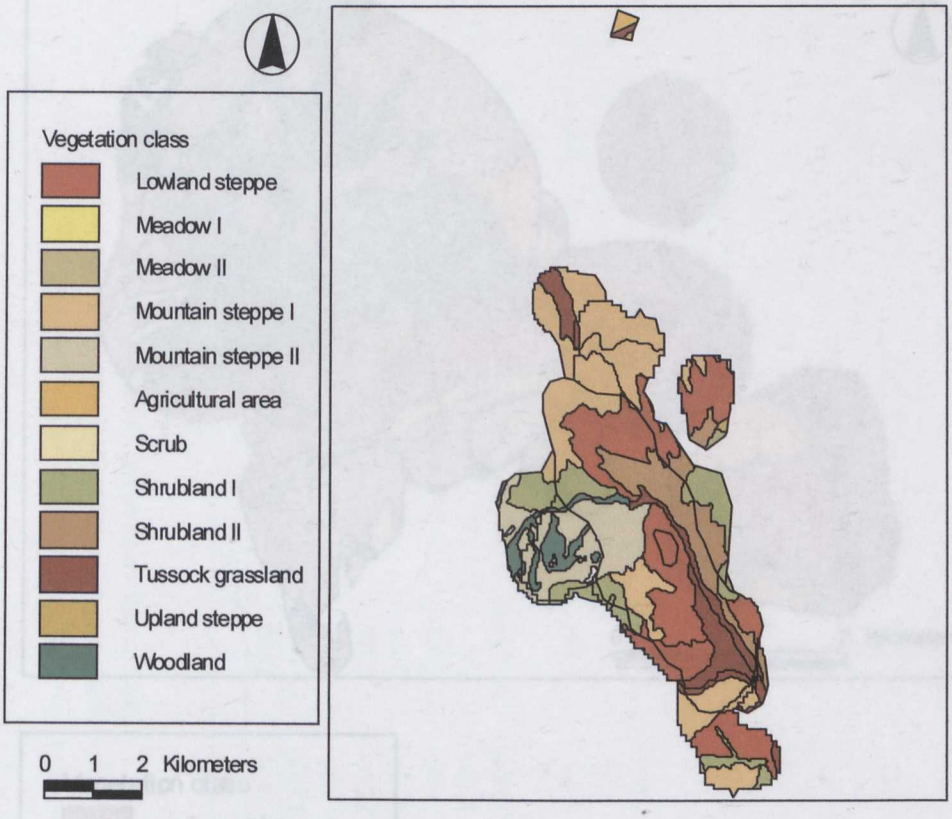
Table 3.11. Vegetation classes at HNP according to landscape features and dominant plant species.

Vegetation class	Dominant species		Landscape	Altitude (m)	Aspect
	Scientific name	Common name			
Meadow I	*Iris lactea*	Dawrf iris	Streamside	1100-1400	
Tussock grassland	*Achnatherum splendens*	Needlegrass	Valley terrace	1100-1400	
Lowland steppe	*Artemisia adamsii - Stipa krylovii*	Wormwood - needlegrass	Footslope	1100-1400	south
Upland steppe	*Thermopsis lanceolatus - Stipa krylovii*	False lupin - needlegrass	Footslope	1300-1500	south
Shrubland I	*Caryopteris mongholica - Amygdalus pedunculata*	Bluebeard - sweet almond	Rocky slope	1300-1600	south
Mountain steppe I	*Festucs lenensis*	Tundra fecue	Ridge & topslope	>1300	
Mountain steppe II	*Festuca siberica*	Siberian fescue	Mountain slope	>1400	north
Shrubland II	*Spiraea aquilegifolia*	Spiraea	Gully	1100-1600	
Meadow II	*Geranium pratense*	Meadow crane's bill	Combe	>1300	
Woodland	*Betula platyphylla*	Asian white birch	Mountain slope	>1400	north
Scrub	*Betula fusca*	Birch	Topslope	>1400	north

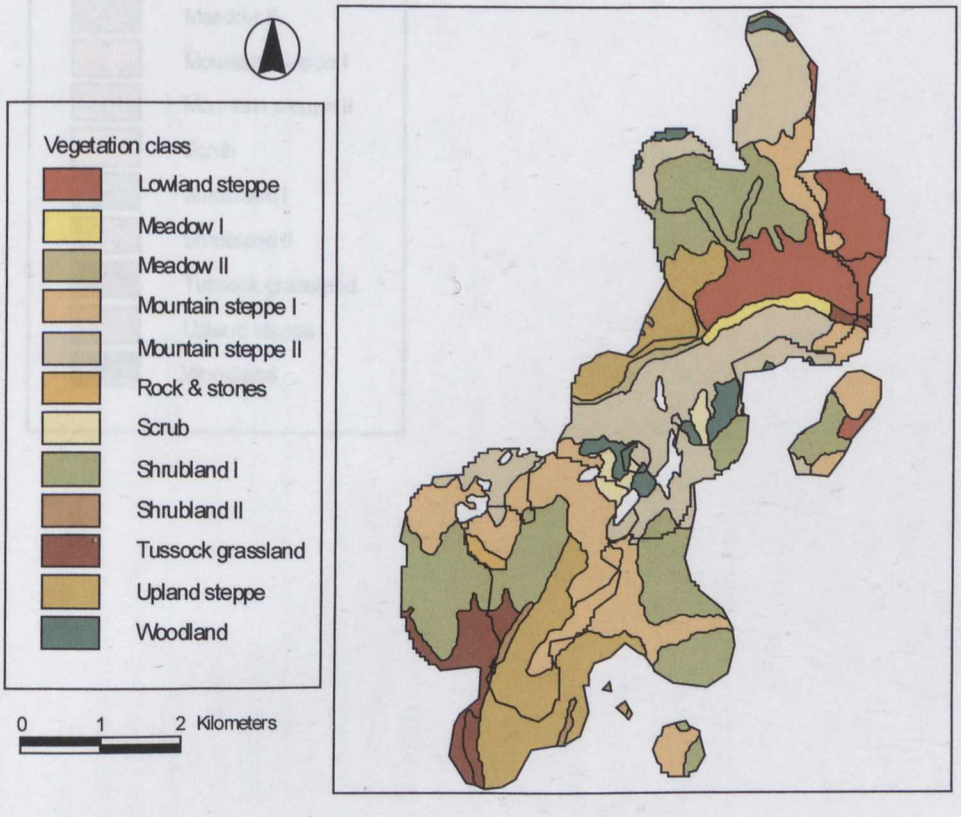
From: Wallis de Vries, M. F., N. Manibazar, and S. Dugerlham. 1996. The vegetation of the forest-steppe region of Hustain Nuruu, Mongolia. Vegetation 122:111-127.

Figure 3.11. Vegetation classes in the home ranges of harems in HNP. Areas shown are home ranges from 1998 to 2000 overlaid on top of one another so the full extent is shown.

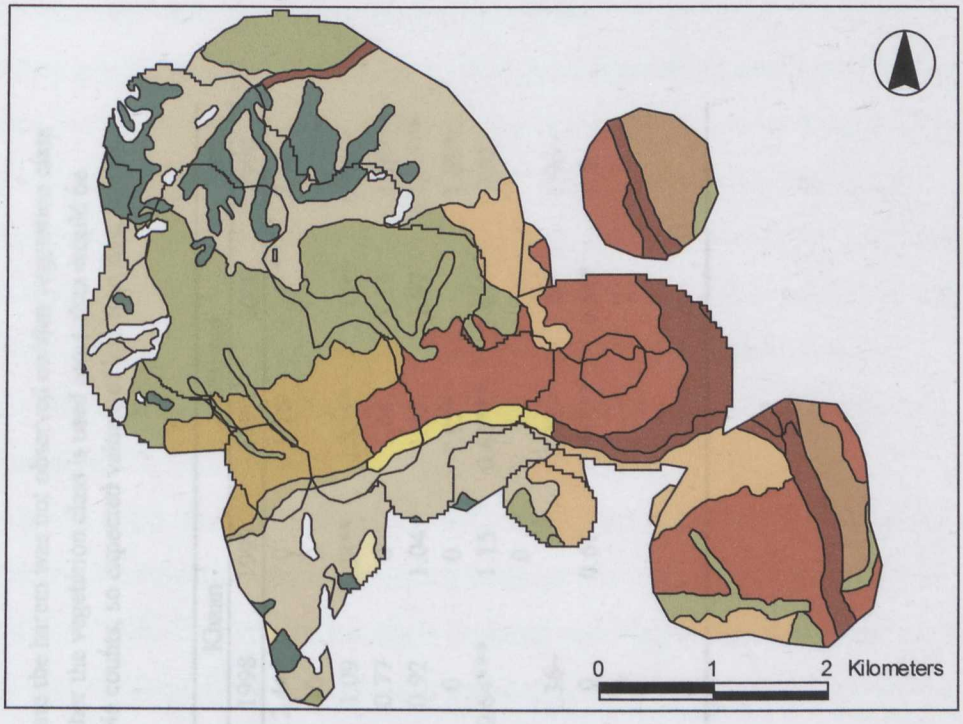
a) Paritet's harem



b) Bayan's harem



c) Khaan and Margad's harems



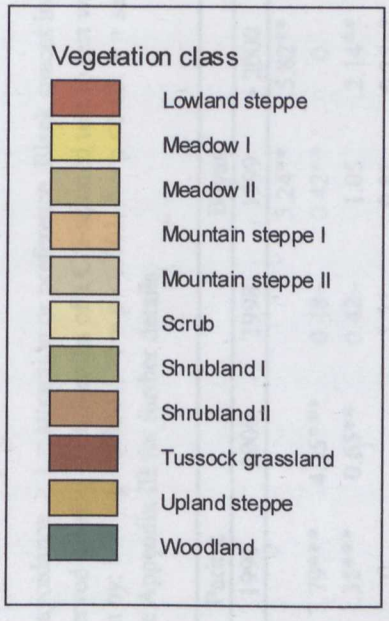


Table 3.12. Habitat (vegetation) selection indices (w_i).

A value of $w_i = 1$ = no selection, <1 = avoidance, > 1 = attraction or preference. Blank spaces indicate the harem was not observed on that vegetation class and a zero indicates they were not observed grazing on it. Results of a Chi-squared test to test whether the vegetation class is used more than would be expected from its availability are shown by: *** = p <0.0001, ** = p <0.001, * = p <0.05. ~ = sample counts, so expected values, of less than five, so the result must be treated with caution. See Appendix III for further details.

Vegetation class	Paritet			Bayan			Khaan		Margad		Ares
	1998	1999	2000	1998	1999	2000	1998	1999	1999	2000	1998
Meadow I					5.24**	5.82**	12.44***	0	1.16	0.34~*	2.25~
Tussock grassland	1.93***	3.79***	4.35***	0.48~	0.42**	0	0	0			
Lowland steppe	1.47*	1.35***	0.65**	0.42~	1.05	2.14**	1.09	2.08**	1.83**	2.75**	0.35~*
Upland steppe		0		1.21	0.81	0.35~*	0.77	0	1.04	1.13	1.76*
Shrubland I	0.66	0.26***	0.61*	0.99	1.88***	1.04	0.92	1.04	1.05	1.07	0.33~***
Mountain steppe I	0.45***	0.66***	0.11***	1.18	0.84	0.53*	0	0	1.85*		1.85*
Mountain steppe II	0.93	0.14***	1.02	0.26~***	0.30***	0.63**	0.64***	1.15	0.61***	0.48**	0.81
Shrubland II	0.35***	0.32***	0.24***	0	1.69~			0			
Meadow II					0	1.02~	1.36~		0.43~	0	1.95~
Woodland	1.48	0.87	0	0	0.47~*	0.77	0	0.61	0.43***	0.51*	0
Scrub				0	0.18~***	0.60~	0				0
Agricultural area		0.29~*									
Rock & stones				0	2.65						

bentgrass (*Agrostis mongholica*) and sedge (*Carex enervis*), as well as *Iris lactea*. In Khaan's home range this vegetation class had been burned in the autumn of 1997 and so had abundant new growth in the spring of 1998.

Tussock grassland was highly selected by Paritet's harem in every year and so appeared to be an important vegetation class for them, possibly because their home range did not include Meadow I vegetation. Tussock grassland contains the needlegrass species *Achnatherum splendens* and *Stipa krylovii* which were shown to have high levels of crude protein (11.3 - 16.8% and 7.3 - 15.6% respectively) as well as crude fibre (27.8 - 28.1% and 24.9 - 27.4% respectively) in HNP by van Dierendonck & Wallis de Vries (1993). Tussock grassland was not found in Khaan/Margad's home range.

Lowland steppe was selected significantly more than most other vegetation classes, and had a high selection index ratio, in all harems except Bayan's in 1999 and Khaan's in 1998. This vegetation class includes the wheatgrass *Agropyron cristatum*, which featured largely in the diets of feral horses, and is dominated by needlegrass (*Stipa krylovii*) which has a high value to the horses as described above.

Both Mountain steppe vegetation classes were found in every home range, and one or both were significantly selected by the harems. These vegetation classes were characterised by the dominant presence of fescues, *Festuca lenensis* in Mountain steppe I, and *Festuca sibirica* in Mountain steppe II. Although these species did not have the high crude protein content of needlegrass (6.1 - 7.0%) they had a higher crude fibre content (31.4 - 31.7%) (van Dierendonck & Wallis de Vries, 1993).

Grazing was observed in Woodland by most harems in most years, and when observed it was selected more than expected from its proportion, but it did not tend to be used more than other vegetation classes. In Woodland the horses appeared to eat the understorey vegetation such as *Spiraea media* and *Cotoneaster melanocarpa*, rather than the trees. The other vegetation classes (Upland steppe, Shrubland I, Shrubland II, Meadow II and Scrub) tended to have sample counts of less than five. As the sample count was low it appears that these vegetation classes were rarely selected, but as the area they covered was small their selection index may be high, thus any results must be treated with caution.

3.2.3.1 Seasonal use of the vegetation

The harems tended to select more vegetation classes in spring and autumn than in summer, and few classes were selected in winter (Table 3.13). From the spring to autumn the horses used the vegetation classes at mid to low elevations, with the only exception being the use of woodland in the spring. In the winter, vegetation at mid elevations was used. Lowland steppe was selected in every season of the year, and Shrubland I and Mountain steppes I and II were selected in every season except winter, showing the importance of the *Stipa* and *Festuca* species for the horses. Both harems observed in winter significantly selected Lowland steppe, and although apparently both also selected another, different, vegetation class, the sample size was too small for this to be reliable. It is interesting to note how Woodland was not used at all in the autumn and winter, and was only selected significantly in the spring. Tussock grassland and Upland steppe were selected by at least two of the three harems in spring and autumn, but not in the summer.

3.2.3.2 Bite rate

The median bite rate over the whole study period was 37 bites minute^{-1} (n = 593, IQR = 31-43). There was no difference in the bite rate among the ages and sexes (H = 2.88, df = 2, p = 0.2373). However, pregnant or lactating mares had a higher bite rate than mares without a foal (Mann-Whitney U = 10920, p = 0.0372). The bite rate decreased through the year with highest bite rates in April and lowest in November (H = 197.35, df = 7, p = <0.0001). The number of steps the horses made in one minute correlated positively with the number of bites (r_s = 0.36, p = 0.0006).

In 1998 and 1999 there was no difference in the bite rate among the vegetation classes (1998: H = 15.28, df = 9, p = 0.084; 1999: H = 13.15, df = 8, p = 0.107). In 2000 the bite rate was higher in the Tussock vegetation class than Lowland steppe and Shrubland I, and the bite rate in Shrubland I was lower than in Upland steppe (H = 17.73, df = 3, p = 0.001).

Table 3.13. Habitat (vegetation) selection indices (w_i) in different seasons of the year. A value of $w_i = 1$ = no selection, <1 = avoidance, > = attraction or preference. Blank spaces inidcate that the vegetation type was not present in the home range, and zero indicates it was not selected at all. Results of a Chi-squared test (1df) to test the significance of the selection index are shown by: *** = p <0.0001, ** = p <0.001, * = p <0.05. ~ = sample counts, so expected values, of less than five, so the result must be treated with caution.

	Spring			Summer			Autumn			Winter	
Vegetation class	Paritet	Bayan	Khaan/Margad	Paritet	Bayan	Khaan/Margad	Paritet	Bayan	Khaan/Margad	Paritet	Khaan/Margad
Meadow I	0	1.48~	0.89~	0	4.31**	14.58**	0	6.87**	3.35*	0	7.56~
Tussock grassland	4.91***	1.23~	0.05~***	3.54***	0	0	3.75***	1.13	0.06~***	0	0
Lowland steppe	1.01	2.05*	1.72**	1.03	0.10~***	0.58**	1.32**	1.99**	2.22**	2.46**	3.21**
Upland steppe	0	1.74*	3.07**	0	1.62*	1.07	0.22~**	0.15~***	3.61**	0	2.05~
Shrubland I	0.34~**	1.61**	1.66**	0.24***	0.71*	1.38**	0.36**	1.78**	0.79*	1.33~	0.11~**
Mountain steppe I	0.09***	0.47**	0.08~***	0.74*	1.93**	0.06~***	0.94	0.57**	0.78	0.24~**	0.47~
Mountain steppe II	0.76*	0	0.34***	0.56**	0.69*	1.14	0	0.16***	0.37**	0	0.69
Shrubland II	0.13	5.15~	0	0.75	0	0	0	1.26~	0	0	0
Meadow II		0	0		1.17~	0.78~		0	2.30~		0
Woodland	0.91	0.16~**	0.31**	0.91	0.76	0.84	0	0	0	0	0
Scrub		0	0		0.60~	0		0	0		0

3.3 DISCUSSION

3.3.1 Home range use

The home ranges of the harems in HNP appear similar to the home ranges of feral horse populations in comparable conditions, in terms of their size and use (Table 3.1). These populations consist of those in the American west (Berger, 1977, 1986; Feist & McCullough, 1976; Miller, 1983b; Pellegrini, 1971), and those in Alberta, Canada (Salter & Hudson, 1982) and the Kaimanawa Range of New Zealand (Linklater *et al.*, 2000). Home ranges of horses in England (Gates, 1979; Tyler, 1972), and barrier islands (Keiper, 1976; Rubenstein, 1981; Zervanos & Keiper, 1979) had smaller home ranges than at HNP, lending weight to the hypothesis that home range size is dependent on the quality of the vegetation and the distribution of resources (Leuthold, 1977). In contrast the home ranges of other equids do not appear to be similar in size. Asiatic asses in Israel (Saltz *et al.*, 2000), and mountain zebras in South Africa (Penzhorn, 1982b) had smaller home ranges than the Przewalski horses. The plains zebra (Klingel, 1969) appears to have a much larger home range as their migration route was included in the calculation. If they are examined at either end of their migration when they are more sedentary their home ranges may be more similar to other equids.

There appeared to be no trend in change of home range size since release, or with harem size at HNP. It is therefore difficult to predict if or how the ranges will change in size. Ultimately this is likely to depend on the amount of forage available in relation to the grazing pressure, and also on environmental factors. Mongolia has suffered from droughts and unusually severe winters recently, which will affect the vegetation growth. It is possible that ranges will reduce at times when forage quality is good, as the home ranges of reintroduced Arabian oryx became smaller around areas where rain had fallen (Corp *et al.*, 1998). Other studies on feral horses have shown a positive correlation between home range and harem size (Berger, 1986; Linklater *et al.*, 2000; Zervanos & Keiper, 1979). Possibly this will have more effect at HNP in the future when more horses will be using, and possibly competing for, resources. Larger harems have been shown to have priority of access to water holes (Miller & Deniston, 1979), and also tend to be found in the areas of better vegetation (Berger, 1986), possibly

because larger harems are thought to be dominant over smaller harems (Miller & Deniston, 1979).

The horses at HNP have a density comparable to feral horses in the western United States, i.e. from 0.1 horses km^{-2} to 3 horses km^{-2} (Linklater, 2000). Densities of 8 horses km^{-2} and above are found in wild equid populations, but tend to occur in managed populations such as the Camargue (Duncan, 1992a) or the New Forest (Tyler, 1972), or unmanaged island populations (Franke Stevens, 1990; Rubenstein, 1981). In the free ranging Przewalski horse population at HNP it is likely that horses will establish home ranges around or outside the edges of the park before this density is reached. More comparable feral horse populations have a density similar to HNP of around 1.5 horses km^{-2}, and it is likely that this density will be maintained within a home range. With increasing overlap as the population grows the density of horses within the park as a whole will grow, although it is unlikely to exceed 3 horses km^{-2}, the maximum density of feral horses seen in a similar habitat (Berger, 1986).

Bouman (1998) states that the carrying capacity of HNP for Przewalski horses is likely to be about 500 animals (0.9 horses km^{-2}) which is within the densities of horses seen in the western rangelands of America. Care needs to be taken on setting a carrying capacity at HNP as it is crucial that the horses remain within the park boundaries. Measurements of the phytomass of HNP indicated a mean forage availability of 87 g m^{-2} (van Dierendonck & Wallis de Vries, 1993) which equated to 14 large herbivore units (LHU) km^{-2} with 30% use, (although the authors stress that this is a crude estimate of the herbivore carrying capacity), and in 1980 there was a density of 7 LHU km^{-2} in Töv aimak (the administrative region of Mongolia where HNP is located). Although these figures can provide an idea of the ultimate carrying capacity of HNP they cannot be used to suggest the number of Przewalski horses that can be supported. The above figures refer to domestic livestock, which are moved large distances throughout the year to avoid overgrazing of any particular pasture. It appears that the Przewalski horses are unlikely to do this as they remain in the area of their home ranges from one year to the next. These figures also do not take into account the social structure of Przewalski horses, which cannot be grouped into large herds as domestic horses are managed, and so will require more space per horse than domestics. Should the vegetation become denuded it is likely that the horses will increase their home range size, rather than move to a new area.

The Przewalski horse population at HNP will be dependent on the permanent water sources as it grows and colonises further valleys. Availability of water is therefore likely to limit where ranges will be established. Water sources are not present in all valleys (Figure 2.1), and some of the streams in the park are ephemeral. This means that not all valleys will be suitable for colonisation by horses. In addition, it is unlikely that all parts of the park will be used equally due to the nature of the topography and vegetation of the area. Therefore it is likely that horses will start to move out of the protected area even before a density of 0.9 horses km^{-2} is reached.

It is hard to predict at what population density horses, particularly dispersing juveniles, will leave the park, but it is very important to monitor the growing population to find when this begins to occur. It is also important to develop a strategy now to decide how or if to manage the population as it expands beyond the park boundary. Hybridisation with domestic horses is possible and likely, especially as the local people would prize hybrid offspring. There is therefore a need to recognise all hybrids immediately and either have them neutered, or at least ensure they did not re-join the pure population. Mongolian owners of a hybrid would rigorously oppose neutering, as Przewalski horses and their hybrids are thought to be stronger than domestic horses, so they would aim to use it to increase the value of their stock.

As more harems are established in HNP it is probable that overlap between the home ranges will increase. Almost all other studies of feral horses have shown extensive spatial overlap between home ranges (e.g. Berger (1986), Keiper (1976), Linklater *et al.* (2000), Miller (1983b)), yet the horses appear to avoid each other temporally, as at HNP (pers. obs). Following release the harems tended to remain in close proximity to the release enclosure in the first year, then moved a little further away to settle in a valley. Initially the harems selected valleys that were visually separated from each other, but as the population increases and more overlap occurs, more valleys will be colonised and smaller ridges within a valley may be used to separate the harems. It is likely that the horses will tolerate a greater spatial overlap as the population increases, as long as temporal differences of visual space can be maintained. In the winter the harems seemed more tolerant of close proximity to each other (pers. comm. Mongolian rangers), but more work needs to be done on their temporal and spatial relations in this season.

3.3.2 Time budgets

The tendency to graze in the morning and evening and rest through the middle of the day has been widely reported (Table 3.2a), and seasonal differences are commonly shown (Table 3.2b) as horses eat more and rest less in the cooler months. These same daily and seasonal patterns of behaviour, and range and vegetation use were seen in the Przewalski horses at HNP. Feral horses were observed to move from grazing in the valleys to rest on ridges in summer, and have a tendency to spend more time at lower elevations in the winter (Berger, 1986). Physiological needs will drive the horses to spend more time eating in the spring and autumn (Waring, 1983), thus they move less and spend more time at lower elevations. In the winter the horses will need to cover a larger area to find sufficient food and shelter, as has been seen in other studies under similar conditions (Berger, 1977; Linklater *et al.*, 2000). Large ranges in the summer (Berger, 1986), or the spring and autumn (Miller, 1983b), are probably due to topographical features of these areas which mean the horses need to move greater distances to find water or shelter from flies in summer, and to find the best grazing in spring and autumn. Smaller home ranges and less time eating during the day in the summer was seen in this study, as in others (Table 3.1 and 3.2b). At this time of year the horses spent more time at higher elevations as they moved up to ridges to ameliorate the effects of flies. Flies, along with vegetation quality, have a strong effect on horses use of a habitat (Duncan, 1983).

The time budget of horses that had been free ranging for several years was more similar to other studies than the more newly released harems, thus suggesting that time is needed for the horses to adjust. Thus, time since release appeared to affect the time budget of the horses. Different results were obtained by Boyd (1998), (who observed a stallion (Khaan) in the two weeks before and the first two weeks after release in HNP) than in this study, where horses were observed in their first to fifth year free ranging. The most noticeable change in the time budget of the stallion after release from the acclimatisation enclosure was the increase in time he spent moving and the decrease in the amount of time spent stand resting (Boyd, 1998). The amount of time the horses were observed moving in this study was neither as great as Boyd (1998) observed in the stallion after release, nor as little as when he was enclosed (Table 3.2a and Table 3.9a). Thus it is possible that the movement of the stallion was due to an initial exploratory phase. Boyd (1998) also observed less stand resting in the stallion immediately after release than before, but the amount of time the horses spent stand

resting over the first year of release in this study was more similar to when the stallion was enclosed, suggesting that they became more relaxed.

After release the horses will have to adapt to life on the steppes, and cope with the stresses of establishing a home range and a place in the dominance hierarchy of the population. This is bound to have an effect on their daily time budgets. Although Boyd (1998) found no difference in the amount of time spent feeding before and immediately after release, over the year after release newer released harems spent less time feeding than established harems. This could be due to stress, disturbance or greater vigilance of the newly released animals. Over the first year the newly released harems also appeared to rest more than established harems did. It is possible they need to spend more time resting to assimilate the new information during sleep and to recover from stress (Carson & Wood-Gush, 1983b; Dukas & Clark, 1995), or that they need time to alter their resting schedule.

There were few differences in the time budgets of horses of different ages and sexes. The main difference was that foals and juveniles spent more time in recumbent rest than adults, as is common in most animals, including horses (Waring, 1983). Most young animals need to rest more, and although REM sleep can be obtained in horses while stand resting, it can usually only occur while recumbent (Waring, 1983). Foals normally devote a great deal of time to recumbent rest in their early months, but spend less time lying down as their first year progresses (Boyd, 1988a). Lying down was rarely seen in adult horses in this population, as in others (Table 3.2b) and the majority of some harems were not observed to lie down during the day at all in some years. Other studies have reported that at least one horse, usually the stallion or most dominant, would remain standing while the majority was recumbent (Feist & McCullough, 1976; Keiper *et al.*, 1980; King, 1996). This was not always observed at HNP (pers. obs.).

Although there was no difference in the time budget of pregnant or lactating mares and those without foals, pregnant or lactating mares had a higher bite rate when grazing. This implies that although they spent the same amount of time eating they consumed more in a single feeding bout than a mare without a foal. The time budgets between the two mare classes were only examined in 2000, whereas the bite rate data also includes 1999. It is therefore possible that, if the time budgets of mares over a greater sampling period were examined, then differences within the larger data set would become apparent.

The number of horses in the harem had a positive relationship with grazing, and a negative one with stand resting. The fact that larger harems can spend more time grazing would follow the many eyes hypothesis where each individual is able to spend more time feeding, yet less time vigilant, whereas in a smaller group an individual would have to devote more time to vigilance (Quenette, 1990). This will be discussed in more detail in Chapter 4. Less time spent stand resting in larger harems could be due to increased social stress. Alternatively, as grazing and stand resting take up the majority of a horse's time budget, if they are spending more time grazing they simply may not have time to rest.

The behaviour of individuals within the harems at HNP seem to be well synchronised, and all harems were equally synchronous. This can be crucial for the survival of a harem, as they will be at less risk from predation in a cohesive group. The level of synchronicity can also provide an indication of how well adapted the horses are to their environment. A study of the synchronisation of two harems in their acclimatisation enclosures in 1994, using a similar index, showed a level of 57% and 65% (van Dierendonck *et al.*, 1996), whereas all three harems in this study had a mean level of 75%, implying that free ranging harems live as a tighter group.
There was no difference between the synchronicity of the stallion with the harem and that within the harem as a whole, suggesting that the stallion does not necessarily initiate the activity of the harem and so is unlikely to directly lead the harem. Interestingly, the most recently released harem was most synchronous with their stallion.

Predictably the horses were most synchronous during the middle of the day, when resting, and in the morning and evenings, when grazing. Juvenile offspring and their mothers were more synchronous than the harem as a whole. It is likely that the younger animals will learn from the older, and rely on cues from them to know when to move with the group. However, mother-foal dyads were less synchronous than the harem as a whole. The foals analysed for these data were all less than three months old, and they do not begin to have a time budget approximating an adult until they are five months old (Boyd, 1988a). By three months a foal will be beginning to play and explore, but will still be spending a lot of time resting (recumbent rest was excluded from the analysis). Any difference in behaviour between a foal and its mother must therefore be due to the foal following different patterns of behaviour to its mother, as its cycle of sleeping and eating will be much shorter than an adult's.

3.3.3 Vegetation use

Many plants change in nutrition and palatability through the year (Novellie & Winkler, 1993), and in HNP it was found that the horses preferred some species in their early development stages, and avoided others after they had flowered (Enkhee, 1998). Many studies have shown a difference in the habitat use of horses in different seasons (Enkhee, 1998; Miller, 1983a; Putman *et al.*, 1987; Salter & Hudson, 1979), and the horses will seek the best quality vegetation available (Duncan, 1983; Miller, 1983a). Therefore the vegetation available to them probably in part determines the altitudinal movements of the horses through the year. In the winter the horses spent more time at lower or mid elevations, possibly to shelter from inclement weather, but that is also where the most nutritious vegetation was found in Lowland steppe. In Canada, habitat selection in winter was dependent on forage availability (Salter & Hudson, 1978), and the same appears true here. Lowland steppe vegetation was used all year round and is likely to form the basis of the horses' diet when they graze in valleys in the summer. The sample size of observations in winter was small and more work needs to be done on their selection of vegetation in this season, as it is the most crucial time of the year for animals surviving in Mongolia.

The horses all retained good condition throughout the year, and in the spring tended to look better than the local domestic horses (pers. obs.). That the Przewalski horses can successfully survive a Mongolian winter shows that they are able to find and select appropriate vegetation for their needs. The horses selected vegetation classes dominated by grasses and fescues, as seen in other studies of horse diets (Table 3.3). Horses will select the most nutritious vegetation available to them (Duncan, 1992a; Putman *et al.*, 1987) and this was shown at HNP by their selection of vegetation classes containing *Stipa* species, which have a high fibre and crude protein content (van Dierendonck & Wallis de Vries, 1993). Although grazing was observed on all of the vegetation classes overall, the horses did not select all vegetation classes in every year, nor even graze on all vegetation classes present, thus suggesting that they select vegetation to maintain an intake of the highest nutritive value as it changes under different conditions. In 1998 an area of meadow in Khaan's home range had luxurious green growth after being burnt the previous year and was highly selected by Khaan's harem. In the following year when it appeared no different from the surrounding

steppe (pers. obs.) it was not selected at all, possibly as other vegetation was more nutritious than meadow vegetation not enriched by fire.

The rate of food intake of an animal depends on the size of each bite, the bite rate and the time spent foraging (Putman, 1986). There is a negative relation between the vegetation standing crop and the number of bites that an animal will take in a period of time, so as the standing crop of the grass increases the bite rate is likely to decrease (Putman, 1986). In HNP the bite rate of the horses decreased through the year. This was surprising as it would be expected to rise as the productivity of the grass falls in the winter. However this could reflect the height of the vegetation, so increased handling time, through the year, or the fact that the horses needed to eat more to gain weight in the spring than they did in the autumn after being on good forage all summer. The median bite rate of 37 bites minute^{-1} was less than the 51 bites minute^{-1} found by (Negi *et al.*, 1993) in the central Himalayas, which could reflect the relative quality of the standing crop of the vegetation.

The home range size and habitat use of the horses will affect how many animals can be supported by HNP. This study has shown that currently the Przewalski horses are behaving like feral domestic horses in a similar environment, so it would be appropriate to use studies of feral horses to set values of the carrying capacity and grazing pressure of the park. It appears that the horses have adapted to life in Mongolia as they maintain a time budget and a daily and seasonal pattern of habitat use similar to that seen in other equid populations. Each harem lives in a home range with access to food, water and shelter and it is likely that the small changes in range size and shape are due to different factors affecting the vegetation. The horses select certain vegetation classes more than would be expected from the area they cover, and from the dominant species it appears that the most nutritious classes are being chosen. There is a difference in the vegetation selected through the year, but vegetation use needs to be examined in further detail to find the plant species that are most selected and to examine their nutrient content. As the different harems do not all select the same vegetation class, and use different vegetation classes through the year, there is little risk of overgrazing at the present densities.

3.4 SUMMARY

- Between 1995 and 2000 the harems at HNP had home ranges of between 1.3 and 24.0 km^2 with core areas of between 61 and 499 ha.
- Home ranges tended to be larger in the winter, but the difference was not significant.
- Home ranges were near the release enclosure in the first year after release, then shifted away from the enclosure, although a similar area was used from one year to the next.
- There was overlap between the home ranges, but the harems used the area at different times.
- The horses grazed in the valleys in the morning and evening and stand rested near a ridge through the heat of the day. This pattern was less marked in the spring and autumn when the horses would spend more time feeding at low elevations.
- All home ranges contained a water source, rocky outcrops near a ridge, woodland patches and presumably enough grazing.
- There was a positive relationship between time spent grazing and time since release and harem size, and a negative relationship between time spent stand resting and time since release and harem size.
- The activity of individuals in each harem was synchronous 75% of the time. Mares and their offspring were more likely to be doing the same activity than the harem as a whole, and foals were less likely.
- Lowland steppe was selected by every harem in every year, and in every season. Meadow I and tussock grassland were also highly preferred to other vegetation classes. These were all low to mid elevation vegetation classes. In the spring and autumn more vegetation classes were selected than at any other time of year.
- The median bite rate was 37 bites $minute^{-1}$ over the whole study period and tended to decrease through the year from April to November.

Chapter Four

Social behaviour

Chapter 4. Social behaviour

4.1 INTRODUCTION

4.1.1 Social structure of harems

Equids are social animals and all live in some kind of group, although permanence of membership differs among the species. In the African ass, some sub-species of Asiatic ass and Grevy's zebra the only permanent bond is between a mother and her offspring, yet they are seen to occur in herds (Klingel, 1974). The other equid species live in relatively permanent groups based around harem defence polygyny. At their most simple, harems consist of one stallion with a group of mares. A maximum of 26 mares was observed in the managed population at Exmoor (Gates, 1979), and a harem containing 22 mares was observed in Venezuela (Pacheco & Herrera, 1997), but in most other populations there are between 1 and 15 mares in a harem (Linklater, 2000), with a mean of four (Waring, 1983). The number of stallions maintaining a harem ranges from one, which is most common, to six stallions (Keiper, 1976). Multi-male groups have been observed in most populations of feral horses and normally consist of a dominant stallion and one or more subordinate stallions consorting the mares (Linklater, 2000). When multi-male groups are faced with an intruding stallion there is a tendency for the subordinate of the stallions to fight the intruder, while the dominant stallion herds the mares away (Berger, 1986; Feh, 1999; Linklater *et al.*, 1999). The more dominant stallion of a multi-male group has greater access to the mares, so higher paternity, and the subordinate male is able to produce more offspring than a bachelor (Feh, 1990). However there is presently debate as to whether males form alliances which ensures both have higher paternity than single males, or if the dominant male simply tolerates the subordinate male in the group, who sneaks matings (Feh, 2001; Linklater & Cameron, 2000).

All populations of feral horses also include groups of bachelor males, and sometimes non-permanent mixed sex groups (Linklater, 2000). These groups provide a sink for dispersing juveniles. Both sexes in horses disperse, and this will act to reduce the risk of inbreeding by stallions mating with their daughters (Duncan *et al.*, 1984; Monard &

Duncan, 1996). In fact, Berger and Cunningham (1987) found that horses tended not to mate with familiar animals even when they remained in the same harem. The females normally go on to join a harem or a bachelor male, and the males will remain in the bachelor group until they can attain some mares (Berger, 1986; Penzhorn, 1984).

The membership of harems is normally stable through the year (Linklater, 2000), but stallions change and mares may move from harem to harem either voluntarily or through coercion by the stallion (Keiper, 1979). Although this study did not focus on the movements of horses between harems this information is important in order to be able to predict the demographics of the future population. There are several factors that are likely to affect the cohesiveness of a group and so may affect harem changes. These include agonistic behaviour and associative social behaviour, which were studied in detail.

4.1.2 Agonistic behaviour

A dominance rank hierarchy has been observed within and between harems of almost all horse populations where it has been examined (Linklater, 2000). Dominance within harems has been quantified by threats given and received among the animals (van Dierendonck *et al.*, 1995), and between harems by the winner of fights between the harem stallions and priority of access to resources (Miller & Deniston, 1979). Mares of different harems rarely interact and neither do they interfere during a stallion fight (Berger, 1986). An established dominance hierarchy theoretically enables a lower level of agonistic behaviour to exist, as once each animal knows its position it will not need to fight so hard to maintain it (Franke Stevens, 1988). When animals know the fighting ability of each other they can moderate their response to aggression – if they are likely to win then they escalate the encounter, but if not they withdraw (Clutton-Brock *et al.*, 1982). Fighting is energetically demanding and dangerous, so it would be expected that there would be selection pressure on individuals to minimise its frequency (Clutton-Brock *et al.*, 1982). This requires clear signals, and Rubenstein and Hack (1992) found that stallion vocalisations provide direct information about dominance status regardless of familiarity between the animals. However, even when signals are clear, fights can result in death. In HNP two stallions have died as a result of injuries sustained in fights, and animals weakened from fighting will be more susceptible to predation (Berger, 1983b). There has been little work on the signals of

dominance status among mares, but it is likely that they will be aware of their relative status by constant reinforcement during social interactions.

Aggression in horses has been found to be most frequent between animals of similar ranks (Ellard & Crowell-Davis, 1989), or when a new animal joins the group and fights for a position within the hierarchy (Rutberg, 1990). These animals have most to gain by attaining a higher rank. Rutberg and Greenberg (1990) observed that aggression in feral horses peaked when animals reached their full size. Once they had established a position in the rank hierarchy, aggression declined to a more stable level.

Dominant horses, or harems, have priority of access to resources. Dominant harems had priority at a water hole in the Red Desert, to the extent that subordinate harems sometimes had to wait more than five hours to drink (Miller & Deniston, 1979). Dominant individuals are also likely to be able to monopolise the best food resources, as seen in reindeer (Espmark, 1974), or the best resting places, although this has not been studied in horses. Dominant individuals also have the greatest reproductive success. One study showed that dominant red deer hinds were in better condition and produced more male offspring than subordinate hinds (Clutton-Brock *et al.*, 1986). These dominant hinds will have greater reproductive success, as their sons will be larger and in better condition than a subordinate hind's, and so will be more likely to acquire and hold a harem. These males will thus produce more offspring over their lifetime than a weaker male, or a female. Similar results were found in horses; mares in better condition invested more in their sons in terms of condition, maternal care and costs to future reproduction, whereas mares in poorer condition invested more in daughters (Cameron & Linklater, 2000). Male offspring had higher mortality in nutritionally poor years in the Camargue, and it was found that the birth-sex ratio in the following year were female biased (Monard *et al.*, 1997), suggesting that male foals were more costly to the mother.

Some studies have attributed different aggressive acts to different functions, suggesting that kicks or threats to the rear are defensive, whereas bites, bite threats or fore leg strikes are aggressive behaviours (Wells & von Goldschmidt-Rothschild, 1979). After their analysis, van Dierendonck *et al.* (1995) stated that offensive and defensive behaviours should be treated differently when used to work out a dominance hierarchy. However it is not quite so clear cut as that: mares, for example, may attack with a hind leg kick, or defend themselves with a bite threat, depending on the situation.

A higher level of aggression in Przewalski horses than among domestic horses has been reported (Christensen *et al.*, 2002; Feh, 1988). An effect of domestication may be to reduce aggression, as that would make animals easier to handle (Price, 1999). However the picture is not clear. The high level of aggression among the Przewalski horses studied by Feh (1988) may be due to members of the group being relatively new to each other, and so still in the process of forming a dominance hierarchy, and although they recorded a significant difference in agonistic acts between a Przewalski and domestic stallion group, Christensen *et al.* (2002) came to the conclusion that this was not due to increased aggression, but because the Przewalski horses were more socially active. This study aims to quantify the level of aggression in the free ranging harems and to compare it with data from the literature. It is possible that the level of aggression will change after release of the horses as they adapt to their new environment.

4.1.3 Associative behaviour

Associations between the horses in a group affect the cohesiveness of a harem. Studies have shown that horses tend to have preferred adult partners for grazing and resting (Clutton-Brock *et al.*, 1976; Kimura, 1998), although overall foals remain closer to their mothers than any other horse (Carson & Wood-Gush, 1983a). Although most populations have a stable female membership of harems from one year to the next (Penzhorn, 1984 in mountain zebras, Linklater, 2000 in horses), movement of mares between harems also occurs, even independently of influences of the stallion (Keiper, 1976). It would thus be expected that horses that associate with each other preferentially will move together.

Agonistic behaviour tends to be more common among horses than associative behaviour (Wells & von Goldschmidt-Rothschild, 1979), although this could depend on the population. Keiper and Receveur (1992) recorded more non-aggressive than aggressive behaviour in a group of Przewalski horses in a reserve, but nursing was included in the non-aggressive behaviours so may have biased the results. Feh (1988) recorded less mutual grooming and social behaviour in a group of Przewalski horses in a reserve in Holland than in a population of Camargue horses, but the reverse was seen in a Przewalski population in France (Feh & Carton de Graumont, 1995), and in the Ukraine (Christensen *et al.*, 2002). This suggests that the environment affects the

frequency of associative behaviour, although it may also be influenced by species and kinship.

Non-aggressive behaviour in horses consists of mutual grooming or simply being close to another horse. In horses, mutual grooming occurs between a pair of animals, each rubbing the other with their teeth or lips, and is very rarely not mutual (Boyd & Houpt, 1994). Allogrooming in primates is slightly different therefore, as it is normally carried out by one animal (a groomer) on another (a groomee) (Schino *et al.*, 1988). However the two behaviours are comparable. The function of allogrooming is unclear, but is likely to have developed from a purely hygienic function to have social implications (Dunbar, 1991). Grooming is important in animals to remove loose skin and parasites (Mooring *et al.*, 2000), and mutual grooming is useful to attend areas that cannot be reached by the animal itself. Barton (1985) found that allogrooming tended to focus on areas that the animal could not reach or see and so complemented the animals self grooming.

Mutual grooming may also have an appeasement function (Feist & McCullough, 1976), and act to reduce tension (Penzhorn, 1984). Feh and de Mazieres (1993) found that when mutual grooming occurred in the lower neck/shoulder area, the most commonly groomed part, the heart rate of horses slowed. In primates, allogrooming by a female reduced the frequency of displacement activities in a male, which were taken as a sign of tension (Schino *et al.*, 1988). However despite stallions being the most aggressive members of a harem they tended to participate in least mutual grooming (Keiper, 1988). Therefore the appeasement hypothesis may only be true for mares, or to reduce weaning conflict (Penzhorn, 1984) as mutual grooming often occurs between a mare and her offspring (Joubert, 1972). If mutual grooming is conducted to reduce tension it would be expected to occur at a higher frequency in newly released harems as they would be the most stressed. Although it has been little examined in the literature, there may also be a seasonal effect to mutual grooming. Kimura (1998) and Tyler (1972) both observed more mutual grooming in the summer, as that is when the horses tended to be close together, but Tyler (1972) also observed a peak at times of year when the animals were moulting.

Beside these patterns, there are conflicting results in the literature, such as Clutton-Brock *et al.* (1976) recording higher ranking animals initiating most mutual grooming, whereas Keiper (1988) observed foals initiating more than half of all bouts, and

Keiper and Receveur (1992) found that mares initiated most bouts. This study aims to see whether there are clear patterns in associative behaviour among harem members.

4.1.4 Marking behaviour

Scent marking is observed in all species of animals in which olfaction is a major sense, even though its function is still not always understood (Eisenberg & Kleiman, 1972). Marking behaviour has been recorded in all populations of horses where it was looked for (Linklater, 2000). In horses, marking is normally expressed exclusively by stallions, which have been observed to dung on the same spot whenever it is passed, forming stud piles, which are subsequently sniffed and marked in a ritualised manner, and to urinate or defecate on mare eliminations. A small population of Przewalski horses in a new area provides a good opportunity to examine this behaviour in detail.

In territorial animals, scent marks can be used to provide a means of identifying the territory with its owner, not simply to delineate the boundary (Gosling, 1982). Thus a stranger entering the territory and encountering a scent mark will be able to associate that with an animal bearing the same scent and decide whether to retreat. A similar theory could be applied to non-territorial animals marking the dung of a female. However there is little evidence that animals avoid the marked areas of their conspecifics and in fact are more likely to focus on a marked spot and mark it themselves (Eisenberg & Kleiman, 1972).

Marking to disguise the scent of a female has been hypothesised (Tyler, 1972) and appeared to occur in pronghorn antelopes, in which males hide females to ensure exclusive access (Moodie & Byers, 1989). As not all excretions from females are marked in horses this is unlikely to be the case in this species (Turner *et al.*, 1981). Marking frequently occurs during or after an encounter between conspecifics, and so it is possible that it expresses dominance or intolerance of another individual (Ralls, 1971). Yet again, although this occurs in horses, possibly as a reinforcement of their relative status, marking also occurs when an animal is alone (Salter & Hudson, 1982).

When entering a new or unfamiliar area, animals are likely to mark more (Eisenberg & Kleiman, 1972), so this would be expected to occur in the newly released harems in HNP in contrast to those that had been released for a year or more. Domestic horses tend to avoid eating around places where they have deposited dung (Carson & Wood-Gush, 1983b). This has serious implications for the use of the pasture as areas not covered by dung become overgrazed. In the New Forest, where

the horses use latrine areas, it has led to the formation of heavily grazed 'lawns' and ungrazed 'roughs' (Edwards & Hollis, 1982). No evidence of this behaviour was shown by a bachelor group of Przewalski horses in a reserve in England (Redman, 1996), so it is not expected at HNP.

It is likely that scent marking may have a combination of functions, including orientation within the environment, exchanging of information, and development of the personal odour of an individual or group (Eisenberg & Kleiman, 1972). As marking behaviour of stallions is highly ritualised and ubiquitous in all equid populations it is unlikely to be simply a relict behaviour from territorial ancestors (as proposed by Klingel (1972)), but has an important social significance providing a way to communicate.

4.1.5 Vigilance behaviour

Vigilance behaviour is a vital aspect of life for all animals, but it is important to quantify this in a population reintroduced to an area where predators exist when it is not known how this ability has been impaired by captive breeding. The impact of predation on populations of equid species needs to be examined further as most species are endangered (Duncan, 1992b). Few studies have looked at vigilance in horses, despite the many articles that have been published on other aspects of their behaviour. This might be because most populations live in areas with little predator threat, yet most feral horse populations are hard to approach (Berger, 1986), so must be highly vigilant. In addition there is very little research on the behavioural response of zebras to hunting, even though work has been done on the predators (e.g. Schaller (1976)). In HNP, the Przewalski horses are exposed to predation by wolves and it is important that their response is examined as this could form a major threat to their survival.

In Africa, prey animals know the potential of each predator and so can adapt their flight distance and defensive behaviour to the circumstances (Schaller, 1976). In the absence of predators it appears that there is a basal level of vigilance, although this could be attributed to the animal obtaining cues of food patches or the position of group members (Hunter & Skinner, 1998). Two studies (Hunter & Skinner (1998) and Berger (1999)) found that vigilance was higher in populations suffering predation pressure than those without it. Hunter and Skinner (1998) also found similarities in the behaviour of animals in the two populations. Individuals in both predated and non-

predated populations were more vigilant near the edge of groups than at the centre and more vigilant in small groups than large, but animals in the population without predation spent little time being vigilant and more time feeding. In contrast, Berger and Cunningham (1988) found no difference in the vigilance of bison in sites with and without wolves. Captive animals that have never been exposed to predation showed a vigilance response (Hirsch & Bolles, 1980; McLean *et al.*, 1996) suggesting that this behaviour is innate.

The 'many eyes' hypothesis appears to be supported by several studies (Elgar, 1989; Quenette, 1990), so it would be expected that larger harems would be less vigilant and spend more time feeding than small ones. This study of vigilance should provide information relevant to current theory, but also provide an indication of how well the horses are adapted to conditions in Mongolia.

4.2 RESULTS

4.2.1 Rationale

The harem in one year was a basic sampling unit as the sampling time for each individual in the harem would have been the same over that period. In that way each harem in each year can be treated discretely. For some analyses I wanted to compare harems and years, and to look at overall trends in the data. Therefore because the number of horses varied among harems, and the number of days studied varied, for the purpose of some analyses I created a standard measurement unit across all harems – behaviour horse^{-1} standard dawn to dusk day^{-1}, as described in Methods, Section 2.4.

4.2.2 Agonistic behaviour

For a description of terms see Chapter 2, Section 2.3.2.1.

4.2.2.1 Frequency of aggressive acts

The median frequency of aggressive acts for the whole population over the study period was 0.22 acts horse^{-1} hour^{-1} (n = 988 agonistic interactions, IQR = 0.05-0.48 acts horse^{-1} hour^{-1}. Mean = 0.35 acts horse^{-1} hour^{-1}, sd = 0.46). There was a significant difference in the frequency of aggressive acts among the years; least aggression was observed in 1998 (Kruskal-Wallis H = 9.31, df = 2, p = 0.009). Frequencies of aggression of each harem are shown in Table 4.1.

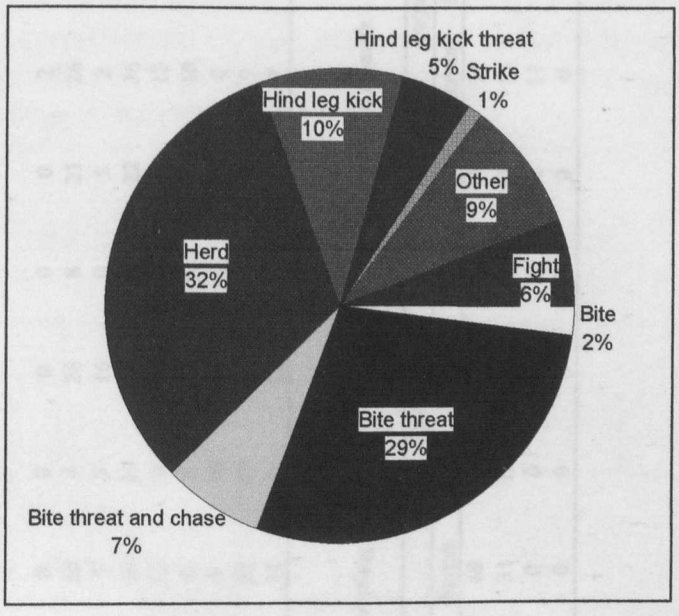
Table 4.1. Frequency of aggression (acts horse^{-1} hour^{-1}) of each harem in each year. Since the data were skewed, median values with IQR in brackets are presented. Means (± 1 sd) are also shown to aid comparison with other studies.

Harem	1998		1999		2000	
	Median	Mean	Median	Mean	Median	Mean
Paritet	0.04 (0.01-0.20)	0.09±0.13	0.58 (0.12-0.78)	0.69±0.81	0.76 (0.38-0.90)	0.68±0.29
Bayan	0.08 (0.04-0.25)	0.13±0.13	0.09 (0.03-0.44)	0.24±0.30	0.20 (0.01-0.36)	0.19±0.18
Khaan	0.10 (0.04-0.33)	0.17±0.15	0.33 (0.12-0.38)	0.28±0.14		
Margad			0.33 (0.20-0.52)	0.34±0.19	0.23 (0.16-0.48)	0.29±0.17
Ares	0.16 (0.06-0.19)	0.14±0.07				

Overall, there was no significant difference in the frequency of aggressive acts among harems ($H = 7.02$, $df = 4$, $p = 0.135$), and there were no significant differences among harems within years (1998 - $H = 1.95$, $df = 3$, $p = 0.583$; 1999 - $H = 4.17$, $df = 3$, $p = 0.244$; 2000 - $H = 4.71$, $df = 2$, $p = 0.095$ (not adjusted for ties)). Only Paritet's harem showed a change in their frequency of aggression among the years, having a lower frequency in 1998 (Paritet - $H = 7.26$, $df = 2$, $p = 0.027$; Bayan – $H = 0.01$, $df = 2$, $p = 0.995$; Khaan – $H = 1.82$, $df = 1$, $p = 0.177$; Margad – $H = 0.42$, $df = 1$, $p = 0.518$). There was no correlation between the harem size and the frequency of aggression in that harem (Pearson's $r = 0.44$, $n = 11$, $p = 0.181$). Thus, overall, all harems had similar frequencies of agonistic acts.

The most frequently observed elements of aggressive behaviour were bite threat, herd, hind leg kick, and 'other' (a combination of behaviours) (Figure 4.1).

Figure 4.1. Behavioural elements observed during aggressive acts. There was a difference among the frequency of the elements used ($X^2 = 882.9$, $df = 8$, $p = <0.0001$).



There was a difference in the frequency of elements of aggressive behaviour seen in the different harems in the different years of the study (Table 4.2). For example, in

Table 4.2. Aggresssive behavioural elements observed in the different harems (%).

	1998				1999				2000		
Behaviour	Paritet	Bayan	Khaan	Ares	Paritet	Bayan	Khaan	Margad	Paritet	Bayan	Margad
n	20	16	58	19	246	44	42	124	278	46	95
Bite	0	0	0	0	0	2	0	1	1	1	0
Bite threat	10	4	26	8	21	26	1	7	11	9	17
Bite threat and chase	5	3	16	0	5	2	0	1	6	1	5
Herd	10	19	14	32	22	36	42	23	37	24	19
Hind leg kick	13	9	17	10	8	10	2	17	9	15	16
Hind leg kick threat	0	6	3	12	8	10	2	4	6	8	7
Fore leg strike	9	10	0	0	0	0	0	2	5	0	3
Fight	22	49	12	13	8	7	34	33	3	0	12
Other	31	0	12	24	28	7	18	13	23	42	20

Table 4.3. Aggressive acts according to age and sex (%), when justified for number of animals.

	1998				1999				2000		
Age/Sex	Paritet	Bayan	Khaan	Ares	Paritet	Bayan	Khaan	Margad	Paritet	Bayan	Margad
Stallion	69	87	75	78	78	75	92	80	84	78	79
Mare	31	13	21	22	18	13	3	14	13	21	19
Juvenile	0	0	3	0	4	11	5	3	2	1	1
Foal	0	0	3	0	0	0	0	3	0	0	1

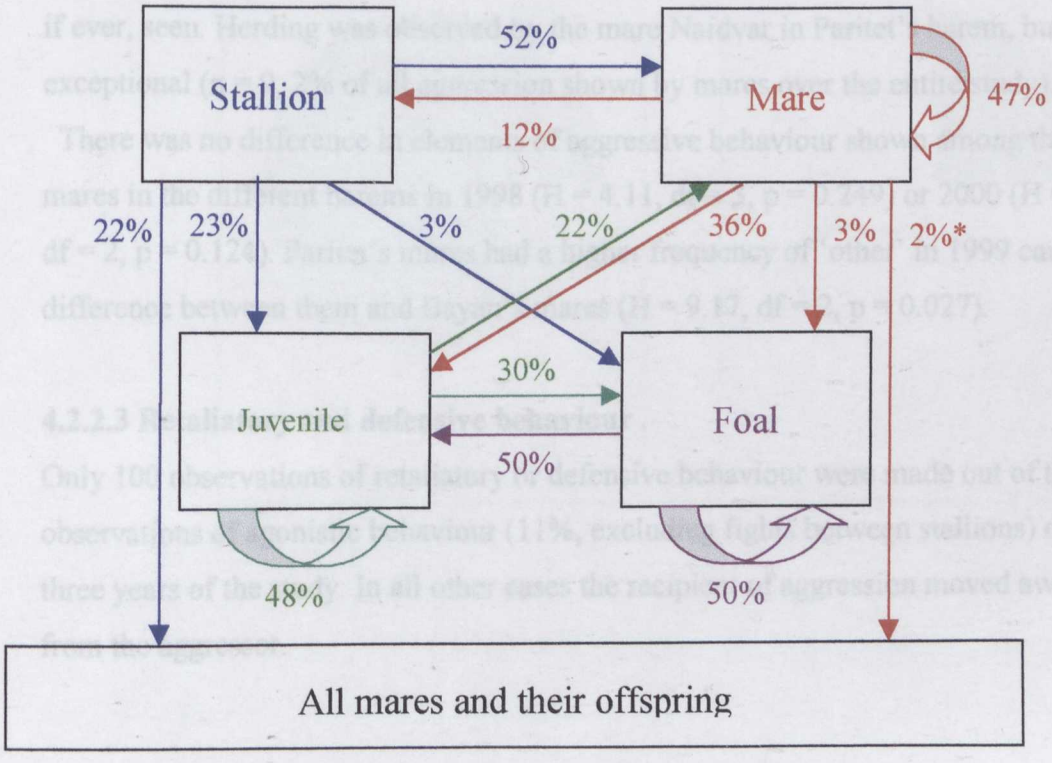
1999 Khaan's harem had low frequencies of most behaviours, but a very high frequency of herd and fight compared to the other harems.

4.2.2.2 Effect of age and sex on aggression

There was a significant difference in the frequency of aggression observed among the different age and sex classes ($X^2 = 138.93$, df = 2, p = <0.0001). Stallions were more aggressive (median = 0.28 aggressive acts hour^{-1}, IQR = 0.06-0.63) than mares (median = 0.06 aggressive acts hour^{-1}, IQR = 0.02-0.14) or juveniles (median = 0 aggressive acts hour^{-1}, IQR = 0-0.02). Aggression by foals was a rare event (n = 4). Stallions had a higher frequency of aggression than mares, and mares more than juveniles in all the harems (Table 4.3).

Stallions aggressed against all other harem members, yet received relatively little aggression, and only from mares (Figure 4.2). All the aggression of stallions directed against all mares in the harem was in the form of herding. Mares also aggressed against all other harem members, but most of their aggression was towards other mares. Juveniles directed a large proportion of their aggression towards foals, but most was to other juveniles. There was no case of a juvenile being aggressive to a stallion.

Figure 4.2. Aggressive acts elicited and received by the different ages and sexes. The percentage values are for pooled harems and years. * - This was a single mare, Naidvar, herding, as will be discussed below.



The stallions expressed different aggressive behavioural elements to mares (X^2 = 562.91, df = 6, p = <0.0001). Stallions were observed herding, fore leg strike and fighting more than the mares, but among mares expressions of bite, bite threat and bite threat and chase, as well as hind leg kick and threat were more frequent than among stallions (Figure 4.3). This trend was observed in each harem in each year (Appendix VIII).

There was no difference in the frequency of aggressive acts among the stallions (H = 0.96, df = 4, p = 0.915), and this did not change among the years (H = 1.17, df = 2, p = 0.558). Of the aggressive behavioural elements, stallions were observed herding more than any other behaviour, although fight and 'other' were also common (X^2 = 1641.38, df = 8, p = <0.0001; Figure 4.3a). Bayan was observed expressing fewer fight and bite elements than Paritet and Margad overall (H = 16.48, df = 4, p = 0.002). There was a difference between Bayan and Paritet in 1999 (H = 10.36, df = 3, p = 0.016), but no difference among the stallions in 1998 (H = 1.07, df = 3, p = 0.785) or 2000 (H = 5.04, df = 2, p = 0.08).

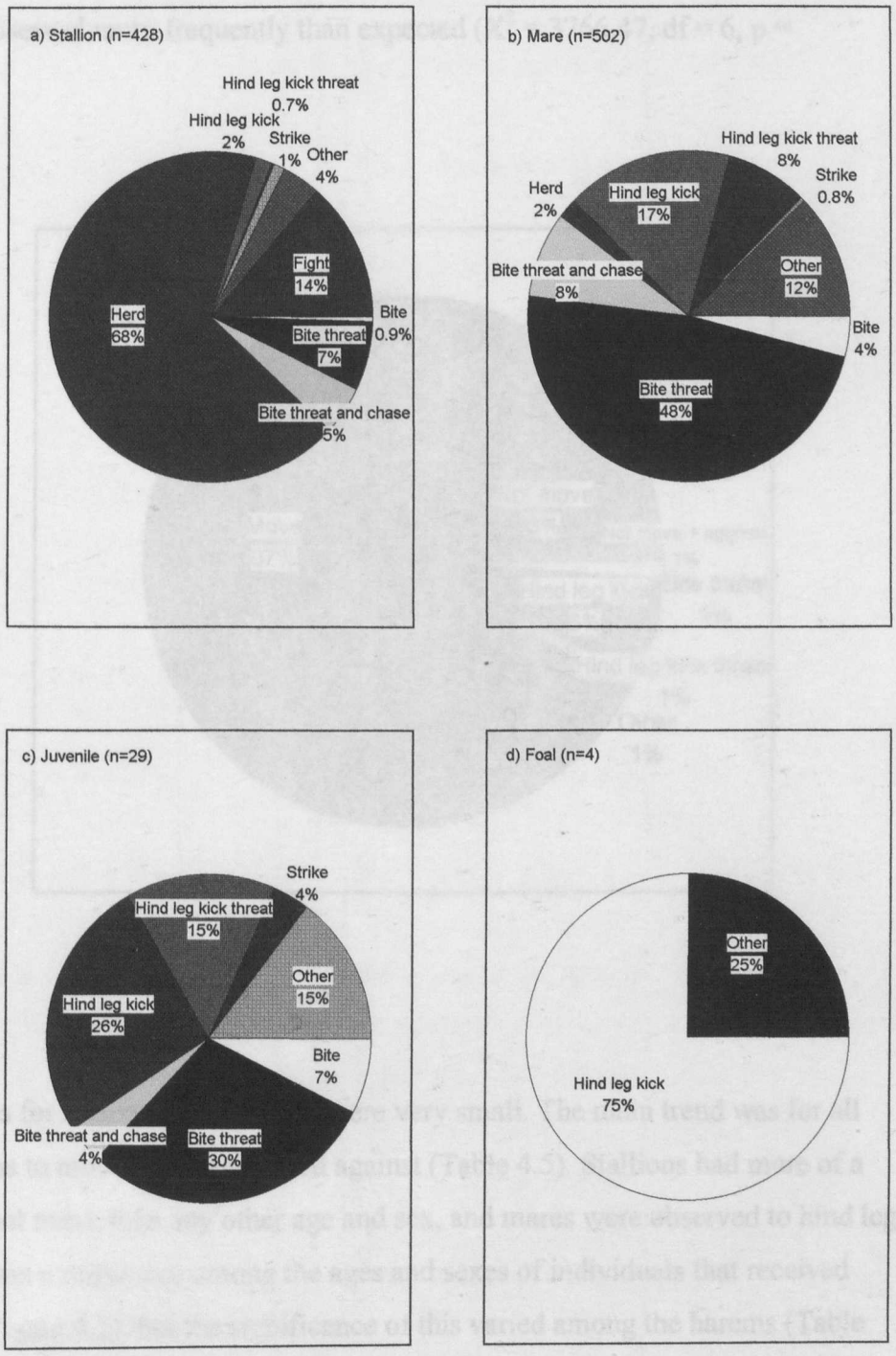
There was no difference in the frequency of aggressive acts among the mares in the different harems (H = 2.71, df = 4, p = 0.608), and the frequency did not change among the years (H = 0.56, df = 2, p = 0.756). Mares were most frequently observed to bite threat and hind leg kick (X^2 = 651.19, df = 7, p = <0.0001; Figure 4.3b). The mares appeared to express a wider repertoire of aggressive behavioural elements than the stallions, although, in contrast to stallions, herding and fore leg strike were rarely, if ever, seen. Herding was observed by the mare Naidvar in Paritet's harem, but was exceptional (n = 9, 2% of all aggression shown by mares over the entire study).

There was no difference in elements of aggressive behaviour shown among the mares in the different harems in 1998 (H = 4.11, df = 3, p = 0.249) or 2000 (H = 4.17, df = 2, p = 0.124). Paritet's mares had a higher frequency of 'other' in 1999 causing a difference between them and Bayan's mares (H = 9.17, df = 2, p = 0.027).

4.2.2.3 Retaliatory and defensive behaviour

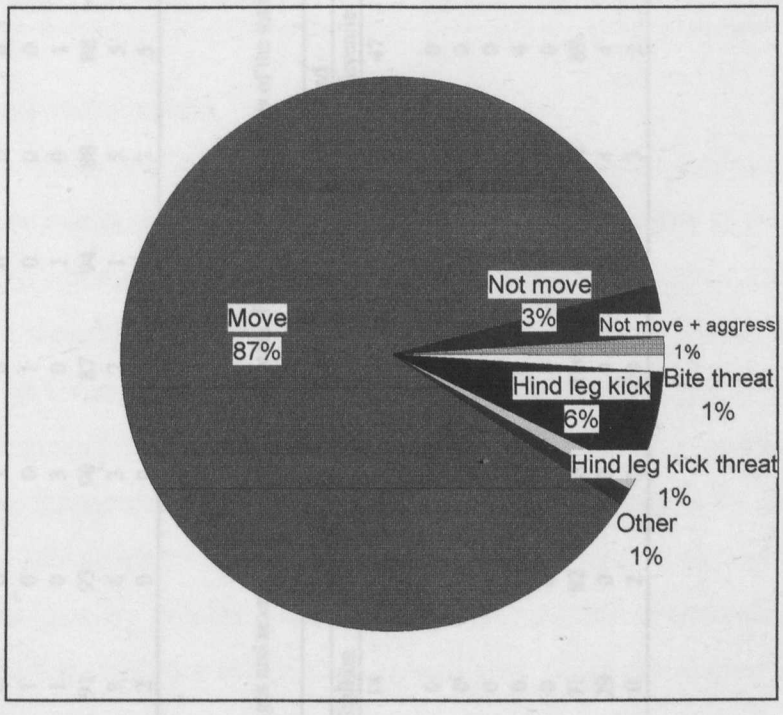
Only 100 observations of retaliatory or defensive behaviour were made out of the 928 observations of agonistic behaviour (11%, excluding fights between stallions) over all three years of the study. In all other cases the recipient of aggression moved away from the aggressor.

Figure 4.3. Agonistic behaviour elements used by each age and sex.



Various behaviours were used by the horses in response to being attacked (Figure 4.4), but the most common behaviour was 'move' (87% of all observations), followed by hind leg kick (6%). This pattern was observed in all harems (Table 4.4).

Figure 4.4. Behavioural elements observed during retaliatory or defensive behaviour. Move was observed more frequently than expected ($X^2 = 3766.47$, df = 6, p = <0.0001).



Sample sizes for retaliatory behaviour were very small. The main trend was for all ages and sexes to move when aggressed against (Table 4.5). Stallions had more of a tendency to not move than any other age and sex, and mares were observed to hind leg kick. There was a difference among the ages and sexes of individuals that received aggression (Figure 4.2), but the significance of this varied among the harems (Table 4.6). The lack of significance in some of the Chi-square tests is probably due to low sample sizes and few degrees of freedom. In all cases the sample sizes of juveniles and foals were too low to be included as aggressors in the contingency table. Overall, mares and juveniles received most aggression ($X^2 = 15.96$, df = 3, p = <0.01).

Table 4.4. Retaliatory and defensive behavioural elements observed in the different harems (%), excluding fights among stallions.

	1998				1999				2000		
Behaviour	Paritet	Bayan	Khaan	Ares	Paritet	Bayan	Khaan	Margad	Paritet	Bayan	Margad
Bite threat	0	0	0	0	0	0	0	0	0	0	0
Hind leg kick	4	3	3	4	2	1	2	3	2	4	2
Hind leg kick threat	3	0	3	0	0	0	1	0	0	0	0
Snap	0	0	2	0	1	0	0	1	0	0	0
Other	5	0	4	5	1	0	3	0	1	0	1
Move	74	87	80	91	91	93	90	87	94	88	88
Not move	7	0	9	0	3	6	3	7	1	5	5
Not move & aggress	7	10	0	0	2	0	0	2	0	3	5

Table 4.5. Retaliatory and defensive behaviour observed from the different ages and sexes in each harem over all years. Figures are percentages of the total of each age and sex, excluding fights among stallions.

	Paritet				Bayan				Margad				Khaan			
Behaviour	Stallion	Mare	Juvenile	Foal	Stallion	Mare	Juvenile	Foal	Stallion	Mare	Juvenile	Foal	Stallion	Mare	Juvenile	Foal
n	25	220	188	23	14	44	18	5	13	110	47	2	4	37	24	1
Bite threat	0	1	0	0	0	0	0	0	0	0	0	0	0	5	0	0
Hind leg kick	0	12	3	0	0	16	0	0	0	10	0	0	0	11	4	0
Hind leg kick threat	0	0	1	0	0	0	0	0	0	0	0	0	0	11	0	0
Snap	0	0	5	4	0	0	11	0	0	0	4	0	0	0	4	0
Other	4	0	0	9	0	0	0	0	0	2	0	0	0	3	0	0
Move	72	84	90	87	71	82	89	100	62	82	89	100	75	65	92	100
Not move	12	1	1	0	29	0	0	0	31	4	4	0	25	5	0	0
Not move & aggress	12	0	1	0	0	2	0	0	8	3	2	0	0	0	0	0

Table 4.6. Results of Chi-squared tests for aggression received. A significant X^2 result showed that the stallion and mare received different amounts of aggression. * - indicates that the contingency table contained expected values of less than 1 so the results should be treated with caution.

Year	Paritet	Bayan	Khaan	Margad	Ares
1998	$X^2 = 1.26$*, df = 1, p = n/s	$X^2 = 3.59$, df = 1, p = 0.058	$X^2 = 3.04$, df = 2, p = 0.219		$X^2 = 7.54$*, df = 2, p = <0.025
1999	$X^2 = 15.44$, df = 6, p = 0.001	$X^2 = 8.88$*, df = 4, p = n/s	$X^2 = 9.53$*, df = 3, p = <0.05	$X^2 = 29.20$, df = 3, p = <0.0001	
2000	$X^2 = 31.93$*, df = 4, p = <0.001	$X^2 = 16.73$, df = 3, p = 0.001		$X^2 = 8.68$, df = 3, p = 0.034	

4.2.2.4 Dominance hierarchies

A dominance hierarchy was drawn up for each harem in each year plotting the winner and loser of every interaction in a matrix (Appendix IX). The linearity of the hierarchies varied among harems and years (Table 4.7) and not all dominance hierarchies were significantly linear. However, except in the case of Bayan's harem, this did not reflect inconsistencies in the rank order, but is more likely to reflect the low sample size causing too many unknown relationships to enable a significantly linear order to be recognised. In these cases the order given is likely to be an approximation of the actual rank order. The stallion was the most dominant animal in all harems except Bayan's in 1998 and 1999. The rank positions of individual mares in the dominance hierarchies of some of the harems were not constant over the years. Juveniles were found at the bottom of the hierarchy in every harem, but in some cases certain juveniles ranked higher than one or more mares (Appendix IX).

It was expected that most aggression would be directed down the hierarchy and that most aggression and retaliation would occur among animals of similar ranks. More aggression (between 74% and 100%) was directed down the hierarchy than up (X^2 = 22.93, df = 10, p = 0.011), and this is also reflected in the DC index of each harem (Table 4.8). However most aggression was directed to animals other than the one next to it in the hierarchy (X^2 = 18.70, df = 10, p = 0.044), as only between 5% and 28% of aggressive acts were to animals of a similar rank (Table 4.8). Thirty five per cent of aggressive acts to an animal next to it in the hierarchy were bite threats and 28% were herding by the stallion to the mare below him. There was no significant difference in retaliatory behaviour whether an animal was aggressive to one that was above it/next to it, or to an animal below it in the hierarchy (X^2 = 11.35, df = 10, p = >0.05),

Table 4.7. Values for the linearity of the dominance hierarchies within harems. Harem = all horses within the harem except foals, adult = horses of three years and older, mare = adult female horses. h = Landau's linearity index and h' = Landau's linearity index corrected for unknown relationships. For these indices 1 = completely linear and 0 = completely random. The probability of linearity (h) is shown with a p value. DC = directional consistency index, 1 = all aggression in one direction, 0 = aggression is randomly directed up and down the hierarchy. Columns in italics should be interpreted with caution as the sample sizes are small.

a) Paritet's harem

Measures of linearity	1998			1999			2000		
	Harem	*Adult*	*Mare*	Harem	Adult	Mare	Harem	Adult	Mare
h	0.23	*0.23*	*0.25*	0.8	0.89	0.84	0.62	0.86	0.79
h'	0.39	*0.4*	*0.5*	0.85	0.92	0.88	0.69	0.9	0.86
DC	0.58	*0.5*	*0.71*	0.92	0.88	0.93	0.96	0.93	0.97
p	0.45	*0.53*	*0.61*	<0.0001	0.002	0.02	<0.0001	0.0014	0.025
No. interactions	19	*16*	*7*	259	176	81	511	255	60

b) Bayan's harem

Measures of linearity	1998		1999			2000		
	Harem	*Mare*	Harem	Adult	*Mare*	Harem	Adult	*Mare*
h	*0.29*	*0.15*	0.37	0.41	*0.29*	0.43	0.51	*0.15*
h'	*0.51*	*0.55*	0.51	0.54	*0.49*	0.57	0.66	*0.4*
DC	*0.6*	*1*	0.92	0.91	*0.86*	0.91	0.85	*1*
p	*0.46*	*0.55*	0.23	0.29	*0.51*	0.07	0.25	*0.71*
No. interactions	*15*	*2*	50	44	*14*	89	52	*7*

c) Margad's harem

Measures of linearity	1999			2000		
	Harem	Adult	Mare	Harem	Adult	Mare
h	0.37	0.94	0.9	0.34	0.67	0.5
h'	0.48	1	1	0.47	0.79	0.68
DC	0.96	0.92	1	0.84	0.79	0.78
p	0.01	0.03	<0.05	0.04	0.017	0.13
No. interactions	240	128	25	110	77	37

d) Khaan's harem

Measures of linearity	1998			1999		
	Harem	Adult	*Mare*	Harem	Adult	*Mare*
h	0.25	0.48	*0.21*	0.39	0.55	*0.1*
h'	0.39	0.65	*0.48*	0.64	0.8	*0.6*
DC	0.86	0.77	*1*	0.97	0.96	*1*
p	0.03	0.07	*0.39*	0.16	0.28	*0.67*
No. interactions	73	43	*11*	79	56	*1*

e) Ares' harem

Measures of linearity	1998		
	Harem	Adult	*Mare*
h	0.86	0.85	*0.7*
h'	0.94	0.95	*0.9*
DC	1	1	*1*
p	0.04	0.14	*0.43*
No. interactions	44	35	*9*

although the sample size of retaliatory behaviour was small, resulting in some cells with expected values of less than 1.

Table 4.8. Direction of aggression within a harem. DC index is the directional consistency, 1 = all aggression in one direction, 0 = aggression is randomly directed up and down the hierarchy.

Harem	Year	% aggression up the hierarchy	% aggression to the next animal in the hierarchy (up or down)	All other aggression (%)	DC index
Paritet	1998	26	21	53	0.58
	1999	7	13	80	0.92
	2000	6	9	86	0.96
Bayan	1998	13	20	67	0.60
	1999	8	15	78	0.92
	2000	15	11	75	0.91
Margad	1999	7	7	87	0.96
	2000	12	11	77	0.84
Khaan	1998	15	9	76	0.86
	1999	6	28	67	0.91
Ares	1998	0	5	95	1.00

Forty six per cent of all aggressive acts up the hierarchy were in the form of hind leg kicks, and 21% were bite threats (Table 4.9). Animals that were aggressive to an animal above it in the hierarchy were more likely to move (76%) than not move and/or retaliate (24%).

Table 4.9. Elements of agonistic behaviour (%) directed up and down the hierarchy.

Behaviour	n	Up the hierarchy	Down the hierarchy
Bite	19	0	2
Bite threat	278	21	32
Bite threat and chase	63	1	7
Herd	305	1	37
Hind leg kick	101	46	8
Hind leg kick threat	46	13	4
Snap	25	100	0
Strike	8	4	1
Other	83	13	9

4.2.2.4a Paritet's harem

In 1998 the dominance hierarchy for Paritet's harem was not significantly linear and had a low h' and DC value (Table 4.7). In 1999 and 2000 the dominance hierarchy was highly significantly linear and had h' and DC values close to 1. Removing

juveniles from the matrix had the effect of increasing the h' value and slightly decreasing the DC value. Therefore the matrix was more linear but aggression was against animals both above and below in the hierarchy. When the mares alone were analysed the h' value was lower, but the DC value was higher than when the harem was looked at as a whole. Therefore the aggression by adults up the dominance hierarchy was mostly directed against the stallion.

In all years Paritet was the most dominant animal, and Naidvar was the most dominant mare in both years she was in the harem (Appendix IXa). Naidvar was the second most dominant mare in Khaan's harem in 1998 and had a high rank when in Paritet's harem after release in 1996 and 1997 (Hovens, 1997). In 1998 Boroo was dominant to Tengis, and Buyana was subordinate to the other mares, but in 1999 and 2000 the first six mares in the hierarchy maintained the same positions. Ayunga was subordinate to all other mares and a yearling in 1999, but became dominant over the juveniles in 2000. Ov's reduction in status in 2000 was related to the increased aggression against him in this year.

4.2.2.4b Bayan's harem

The dominance in Bayan's harem was not significantly linear in any year, therefore the matrices produced must be treated with caution. In 1998 the sample size was very small (n = 15) and so this year should be disregarded. The DC was high in 1999 and 2000 showing that there was relatively little aggression up the hierarchy in those years (Table 4.7). In 1999 there were inconsistencies between Ajarchan and Sergelen, and in 2000 between Ajarchan and Sharga. This means that Ajarchan dominated Sergelen and Sharga, while being below them in the rank order of the harem. However when a hierarchy was created with the stallion excluded there were no inconsistencies among the mares in 1999, and the ranking was changed. This is therefore possibly a more correct ranking (Appendix IXb iii), but, as it is not significantly linear, it must be treated with caution. There was no difference in ranking of the 2000 data when the mares alone were analysed, but the DC index was 1. Zigmee and Delgerekh had the lowest positions in the hierarchy in 1999 when they first joined the harem, but had moved up the hierarchy in 2000 implying that they had become established (Appendix IXb).

4.2.2.4c Margad's harem

Margad's harem had a significantly linear dominance hierarchy and a high DC value in both years they were studied (Table 4.7). When the adult horses and mares alone were examined in a matrix they had the highest possible h' values and high DC values in 1999, showing the hierarchy was completely linear (adult – h' = 1, DC = 0.92, mare – h' = 1, DC = 1). Thus the juveniles were responsible for any deviation from linearity in that year. In 2000 the h' values were higher and the DC values lower for adults and mares than when the harem was looked at as a whole, but the mares alone did not have a significantly linear hierarchy.

The stallion was dominant and Shuurga and Ireedui were high ranking in both years (Appendix IXc). Riska moved up the hierarchy to be the most dominant mare in 2000 from being the second least dominant mare.

4.2.2.4d Khaan's harem

Khaan's harem had a significantly linear dominance hierarchy in 1998 with an h' value near 1, but not in 1999 (1998 - $p = 0.03$, 1999 - $p = 0.16$). The harem had a high DC in both years (Table 4.7). The DC value was lower and the h' value was higher in a matrix of the harem with the juveniles removed, but was not significantly linear ($p = 0.07$). This suggests that interactions among the adults affected the linearity of the dominance hierarchy more than interactions with the juveniles. The stallion was the most dominant animal in both years (Appendix IXd). The most high ranking mares in 1998 (and Ireedui) left Khaan's harem and became high ranking mares in their new harems. Ireedui was the lowest ranking mare in Khaan's harem in both years, but became a high ranking mare when she joined Margad's harem. The other animals remained in similar positions in 1999.

4.2.2.4e Ares' harem

Ares' harem had a significantly linear dominance hierarchy ($p = 0.04$) with a very high h' value and a DC of 1. The h' value remained high and the DC was 1 when the adults and mares were looked at in matrices on their own, but these matrices were not significantly linear (Table 4.7). See Appendix IXe for the dominance hierarchy matrix.

4.2.2.5 Factors affecting dominance

There are many factors that are likely to affect dominance within a harem, such as height and weight, aggressiveness (number of aggressive acts $hour^{-1}$), age, and length of time the animal has been resident in a harem (when a group of mares moved to another harem, the length of time that they had been together was used). Only the latter three factors will be looked at here. These three factors were correlated against position in the dominance hierarchy for each harem in each year.

Over the population as a whole over the entire study period there was a significant negative correlation between position and aggression, age and tenure (Figure 4.5). Thus horses that are more aggressive, older, or that had spent longest in the harem were more likely to be dominant. However nearly 60% of the position in the hierarchy could not be explained by these factors alone. A stepwise regression showed that aggression and age accounted for only 42% of the rank position ($r^2 = 0.42$), and tenure was removed in the first step. In all harems there was a negative correlation between position and the three main factors, but the significance of the correlation varied among harems and years (Appendix X). There was a positive correlation among aggression and age and tenure in almost all harems and years: thus all three factors were related. However, the significantly positive correlation between age and tenure in all harems (except Paritet in 1999) simply reflects that older horses had spent more time in the harem.

The presence of a foal had no effect on the position of a mare in the dominance hierarchy (paired $t = 0.53$, $df = 21$, $p = 0.6$) nor her frequency of aggression (paired $t = 1.20$, $df = 27$, $p = 0.24$). The positions of all mares with foals were tested against those of a similar age and/or position in the hierarchy who did not have a foal.

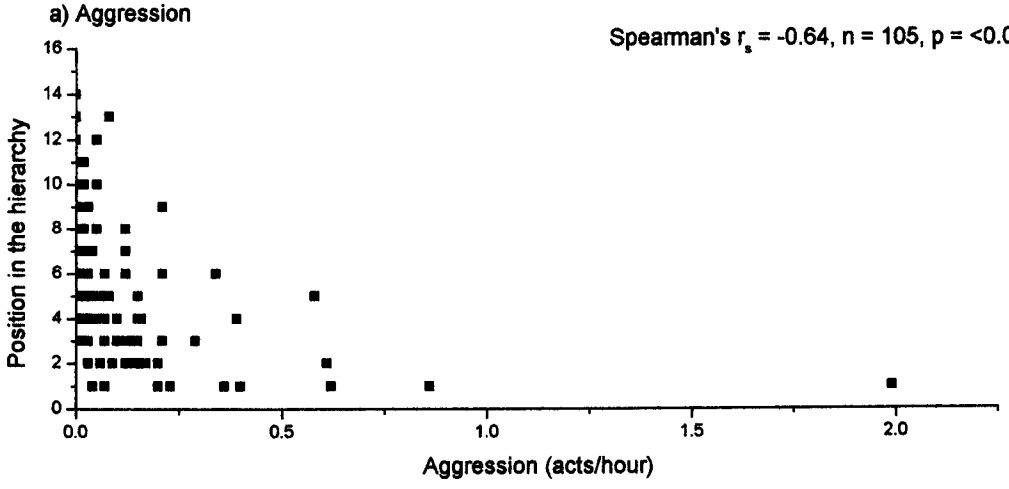
4.2.3 Associative behaviour

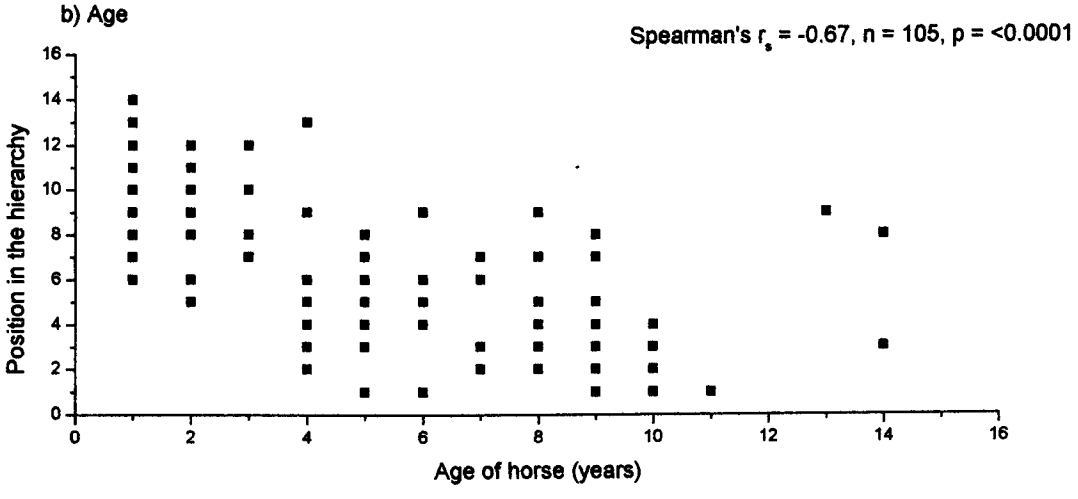
See Chapter 2, Section 2.3.1.3i for a description of terms.

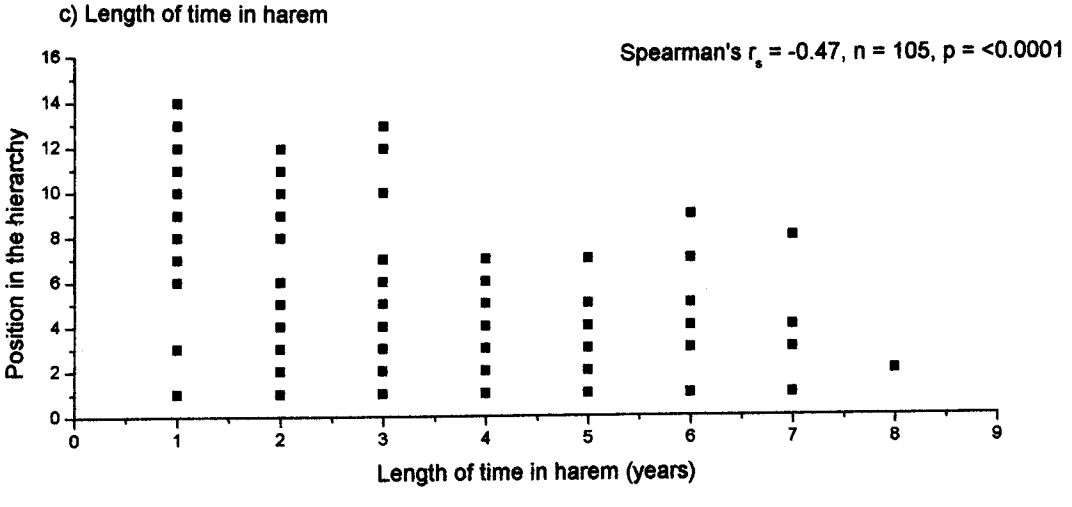
4.2.3.1 Frequency of associative behaviour

Individual associative behaviour elements were observed at a very low frequency, the median frequency of all associative social behavioural acts over all three years was 0.06 acts $horse^{-1}$ $hour^{-1}$ ($n = 773$ acts, IQR = 0.02-0.10. Mean = 0.08, sd = 0.12). There was no significant difference in this frequency between harems ($H = 1.99$, $df = 3$, $p = 0.574$). Mutual grooming and stand resting together (Plates 2.1 and 2.2) were the most

Figure 4.5. Correlation coefficients of a) aggression, b) age and c) length of time in the harem with position in the dominance hierarchy. Position one in the dominance hierarchy is most dominant.







frequent associative behaviours and were observed significantly more frequently than head rubbing or play (Figure 4.6). It is possible that the sampling underestimated the frequency of head rubbing and play because they did not last long when they occurred. Twelve per cent (n = 5) of observations of play were self play. Forty six per cent of play (n = 19) was among foals and juveniles, 12% (n = 5) was between a mare and her juvenile offspring and 29% (n = 12) was between a stallion (Paritet) and his juvenile son (Ov).

There was no correlation between matrices of mutual grooming and stand resting together partners within any harem, suggesting that different partners were chosen for these two activities (Paritet – $r_s = 0.34$, Bayan – $r_s = 0.43$, Margad – $r_s = 0.20$, Khaan – $r_s = 0.24$, all $p > 0.05$).

Most interactions occurred between mares and juveniles ($X^2 = 72820$, df = 8, p = <0.0001) and stallions were only involved in 22% of all interactions (Table 4.10). All observations of stallion and juvenile interactions occurred between Paritet and Ov.

Table 4.10. Associative interactions between ages and sexes. Per cent of the total number of observations (n = 768), or per cent of the total between age/sex pairs that were related (full siblings or offspring) is shown.

Interaction between age or sex class	% Observations	% Related
Mare – Mare	20	1
Mare – Juvenile	40	87
Mare – Foal	4	88
Mare – Stallion	19	0
Stallion – Juvenile	3	100
Stallion – Foal	0	0
Juvenile – Foal	4	10
Juvenile – Juvenile	6	67
Foal – Foal	4	0

4.2.3.2 Mutual grooming

Mutual grooming was observed at a median frequency of 0.02 acts horse^{-1} hour^{-1} (n = 363 acts, IQR = 0–0.06. Mean = 0.04 acts horse^{-1} hour^{-1}, sd = 0.06). Mutual grooming occurred more on the withers (vertebrae at the base of the neck) than any other part of the body (Figure 4.7). There was also a significant difference in the time of day and time of year when there was a higher frequency of mutual grooming (Figure 4.8). Mutual grooming appears more frequent in the spring and autumn, and in the morning

Figure 4.6. Associative behaviours seen in the horses at HNP. Percentage of all behaviour observed is shown. There was a significant difference in the frequency of the behaviours (X^2 = 554, df = 3, p = <0.0001).

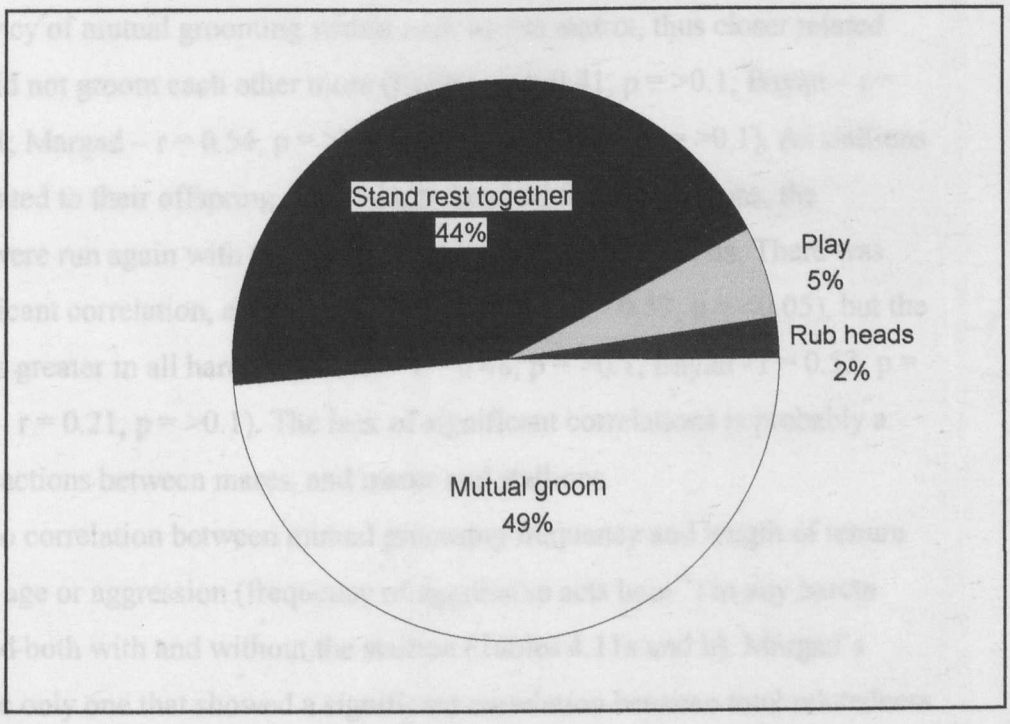
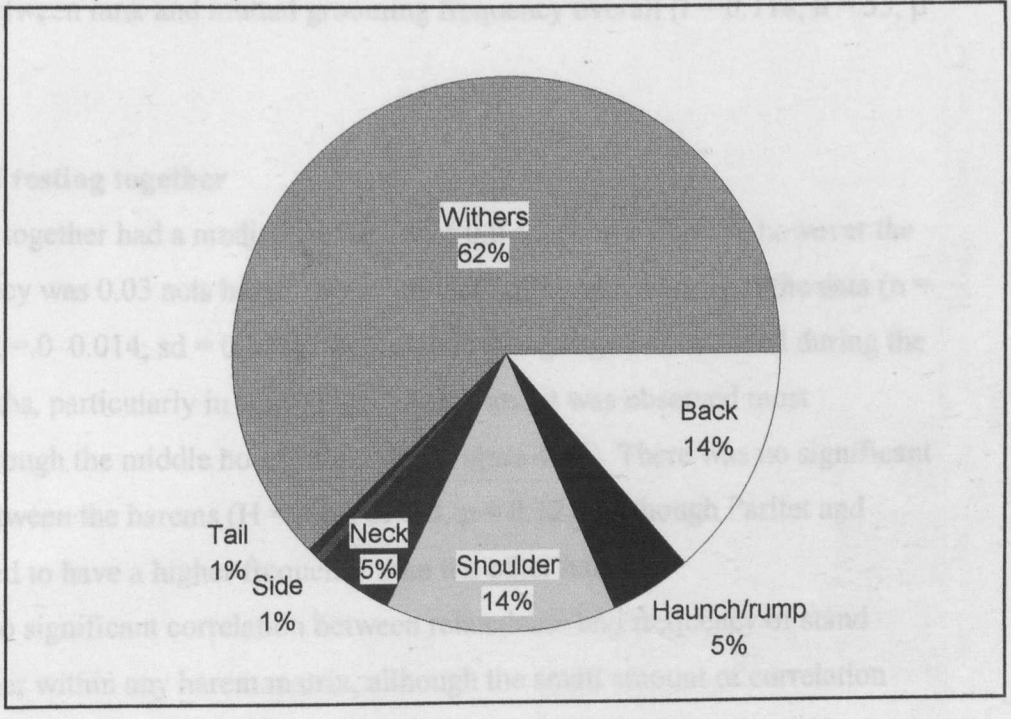


Figure 4.7. Parts of the body observed mutual groomed (percent of the total, n = 373). The withers were groomed significantly more than any other part (X^2 = 746.18, df = 6, p = <0.0001).



and evening (Figures 4.8a and b). There was no significant difference among the harems in the frequency of mutual grooming ($H = 3.30$, $df = 3$, $p = 0.348$).

There was no significant correlation between relatedness (coefficient of relatedness r) and frequency of mutual grooming within each harem matrix, thus closer related individuals did not groom each other more (Paritet – $r = 0.41$, $p = >0.1$; Bayan – $r = 0.31$, $p = >0.1$; Margad – $r = 0.54$, $p = >0.05$; Khaan – $r = 0.15$, $p = >0.1$). As stallions were only related to their offspring, with whom they had few interactions, the correlations were run again with the stallion removed from the analysis. There was still no significant correlation, except in Margad's harem ($r = 0.57$, $p = <0.05$), but the value of r was greater in all harems (Paritet – $r = 0.48$, $p = >0.1$; Bayan - $r = 0.53$, $p = >0.1$; Khaan – $r = 0.21$, $p = >0.1$). The lack of significant correlations is probably a result of interactions between mares, and mares and stallions.

There was no correlation between mutual grooming frequency and length of tenure in the harem, age or aggression (frequency of aggressive acts $hour^{-1}$) in any harem when analysed both with and without the stallion (Tables 4.11a and b). Margad's harem was the only one that showed a significant correlation between total relatedness (quantified as a sum of the coefficient of relatedness with all other harem members) to other members of the harem both with ($r = 0.67$, $n = 13$, $p = 0.013$), and without ($r = 0.67$, $n = 12$, $p = 0.016$), the stallion in the analysis. In addition there was no correlation between rank and mutual grooming frequency overall ($r = 0.118$, $n = 55$, $p = 0.392$).

4.2.3.3 Stand resting together

Stand resting together had a median frequency of 0.0 acts $horse^{-1}$ $hour^{-1}$, however the mean frequency was 0.03 acts $horse^{-1}$ $hour^{-1}$ reflecting the skewedness of the data ($n = 335$ acts, IQR = 0–0.014, $sd = 0.108$). Most stand resting together occurred during the summer months, particularly in May (Figure 4.8c), and it was observed most frequently through the middle hours of the day (Figure 4.8d). There was no significant difference between the harems ($H = 5.82$, $df = 3$, $p = 0.121$), although Paritet and Margad tended to have a higher frequency than the other harems.

There was no significant correlation between relatedness and frequency of stand resting together within any harem matrix, although the small amount of correlation was positive (Paritet – $r_s = 0.35$, $p = >0.1$; Bayan – $r_s = 0.29$, $p = >0.1$; Margad – $r_s =$

Figure 4.8. Effect of hour and month on mutual grooming (hollow bars) and stand resting together (shaded bars). More mutual grooming (X^2 = 227.59, df = 7, p = <0.0001) and stand resting together (X^2 = 585.89, df = 5, p = <0.0001) occurs more at certain months. Mutual grooming (X^2 = 165.16, df = 16, p = <0.0001) and stand resting together (X^2 = 325.98, df = 14, p = <0.0001) were observed more at certain hours of the day.

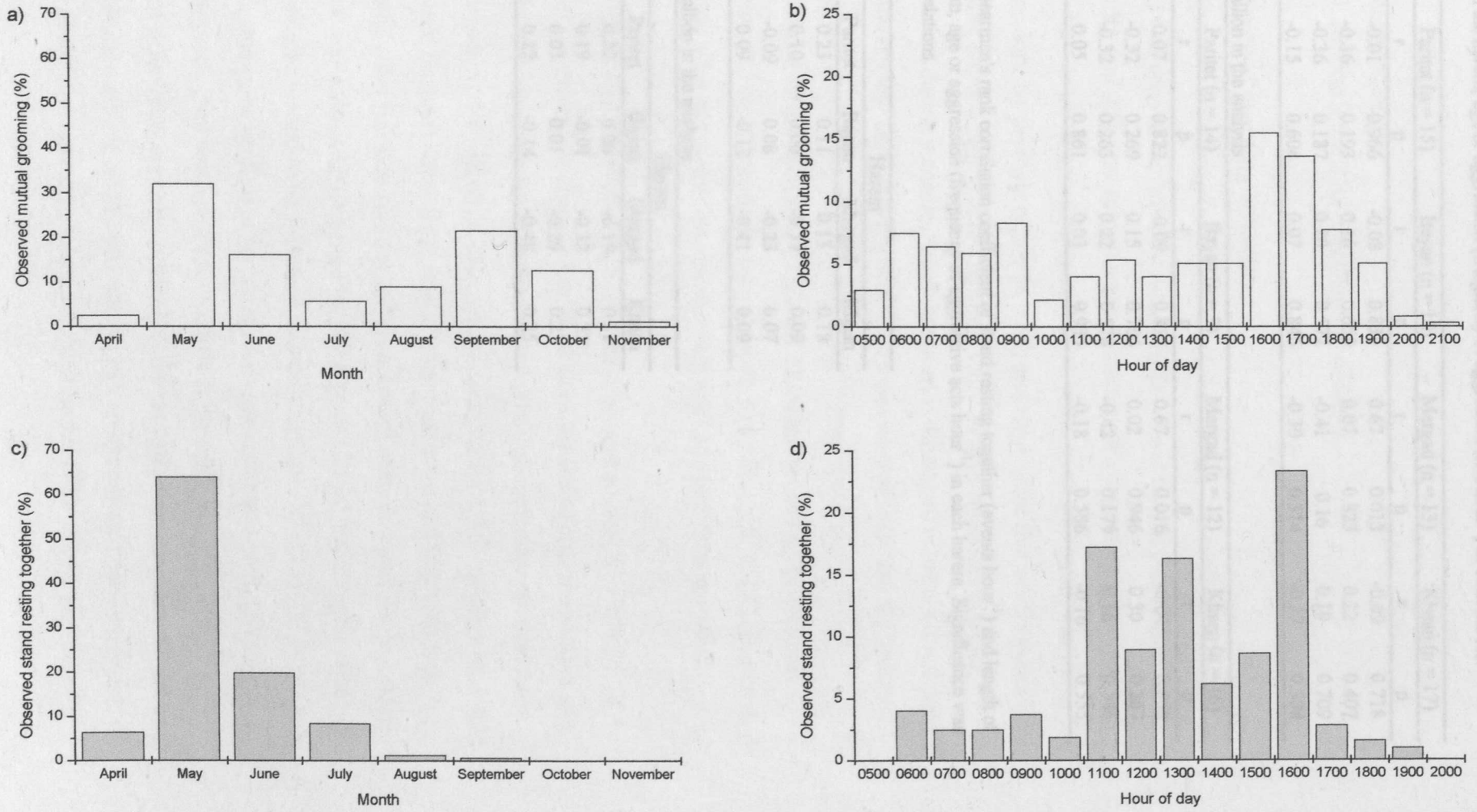


Table 4.11. a). Pearson's correlation coefficient between mutual grooming frequency (events hour^{-1}) and length of tenure in the harem, age or aggression (frequency of aggressive acts hour^{-1}) in each harem.

	Paritet (n = 15)		Bayan (n = 10)		Margad (n = 13)		Khaan (n = 17)	
Factor	r	p	r	p	r	p	r	p
Relatedness	-0.01	0.966	-0.08	0.833	0.67	0.013	-0.09	0.718
Tenure	-0.36	0.193	0.16	0.659	0.07	0.823	0.22	0.407
Age	-0.36	0.187	0.20	0.572	-0.41	0.16	0.10	0.709
Aggression	-0.15	0.604	0.07	0.846	-0.30	0.314	-0.17	0.508

b) Without the stallion in the analysis

	Paritet (n = 14)		Bayan (n = 9)		Margad (n = 12)		Khaan (n = 16)	
Factor	r	p	r	p	r	p	r	p
Relatedness	0.07	0.822	-0.09	0.812	0.67	0.016	-0.04	0.888
Tenure	-0.32	0.269	0.15	0.706	0.02	0.946	0.30	0.267
Age	-0.32	0.263	0.22	0.578	-0.42	0.179	0.16	0.546
Aggression	0.05	0.861	0.03	0.935	-0.18	0.586	-0.16	0.555

Table 4.12. a). Spearman's rank correlation coefficient of stand resting together (events hour^{-1}) and length of tenure in the harem, age or aggression (frequency of aggressive acts hour^{-1}) in each harem. Significance was p=>0.1 in all correlations.

	Harem			
Factor	Paritet	Bayan	Margad	Khaan
Relatedness	0.23	0.11	0.13	0.18
Tenure	0.10	0.06	-0.37	0.09
Age	-0.09	0.08	-0.23	0.07
Aggression	0.09	-0.12	-0.41	0.09

b). Without the stallion in the analysis

	Harem			
Factor	Paritet	Bayan	Margad	Khaan
Relatedness	0.32	0.06	-0.19	0.31
Tenure	0.19	-0.01	-0.32	0.22
Age	0.03	0.01	-0.29	0.23
Aggression	0.22	-0.14	-0.48	0.25

0.14, p = >0.1; Khaan – r_s = 0.08, p = >0.1). There was also no significant correlation between total relatedness, age and tenure for any harem (Table 4.12).

4.2.4 Marking behaviour

See Chapter 2, Section 2.3.2.2 for a description of terms.

4.2.4.1 Frequency of marking behaviour

The mean frequency of marking behaviour was 0.4 acts $hour^{-1}$ (n = 69, sd = 0.38). More marking was seen in the breeding season (May/June) than at other times of the year (Figure 4.9), and different stimuli were marked at this time from other months (Figure 4.10). Almost all marking behaviour observed was conducted by stallions; 5% of marking was done by juvenile males (n = 18) and there were five observations (2%) of mares sniffing either a stud pile or old dung. Only 11% of observed marking behaviour occurred during a confrontation between stallions, all other occurred during the course of the horses' daily movements. There was no evidence that the horses avoided eating near dung or of latrine areas being formed (pers. obs.).

Marking behaviour is summarised in Figure 4.11. When marking, the stallions urinated or defecated more frequently than flehmen or sniffing (X^2 = 242.50, df = 4, p = <0.0001). Stud piles and unknown stimuli were marked more than any other stimulus (X^2 = 143.78, df = 4, p = <0.0001).

There was a significant association between stimulus and action (X^2 = 174.74, df = 12, p = <0.0001). Marking on dirt was excluded from the analysis as the sample size was too small. Defecation tended to occur on stud piles, and urination on unknown and mare eliminations. Not all mare eliminations were marked, but unfortunately data were not gathered on the relative frequency of this. Stud piles and old dung were sniffed most, and most flehmen was caused by unknown stimuli (most likely a mare elimination that was either old, obscured by grass, or deposited out of sight). The different stimuli also tended to be found on different terrains (X^2 = 135.73, df = 6, p = <0.0001), with stud piles tending to occur on roads and paths and mare eliminations being found on grass. Dirt was again excluded from the analysis.

A sequence of behaviours was observed when the stallions marked. They would sniff the stimulus before marking, and/or afterwards, in a characteristic posture (Plate 4.1). The sequence of sniffing tended to vary with the stimulus (X^2 = 70.40, df = 3, p =

Figure 4.9. Observations of marking events in each month.
There was a difference among the months (X^2 = 134.15, df = 7, p = <0.0001).

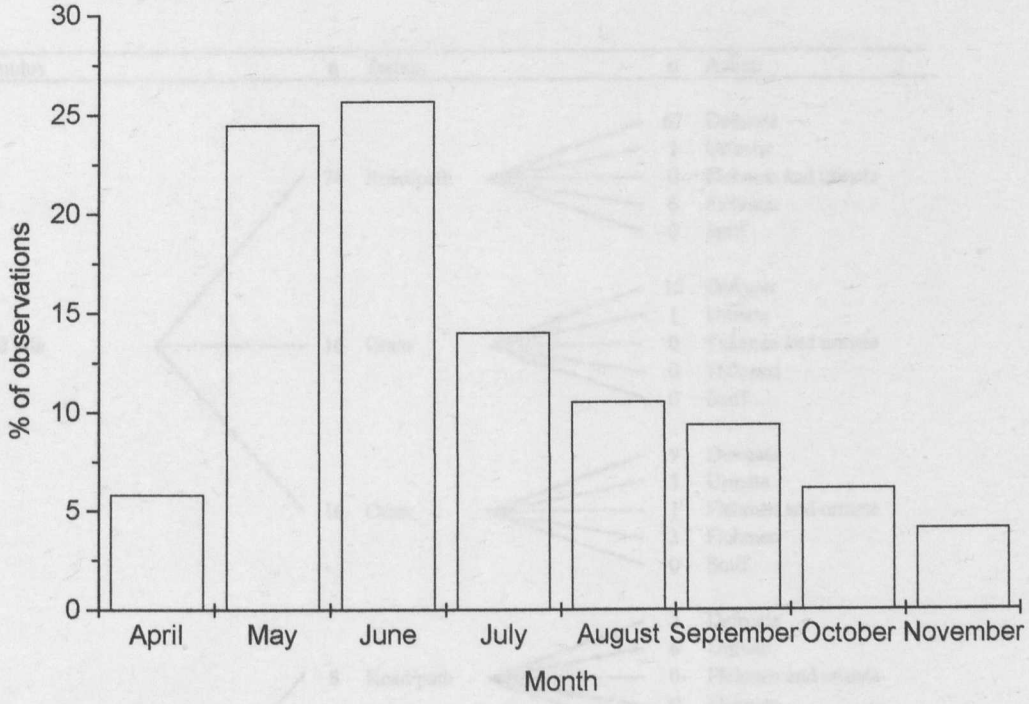


Figure 4.10. Stimuli marked in each month (% of total). Different stimuli were marked in the different months (X^2 = 47.01, df = 21, p = 0.001). Dirt was excluded from the analysis.

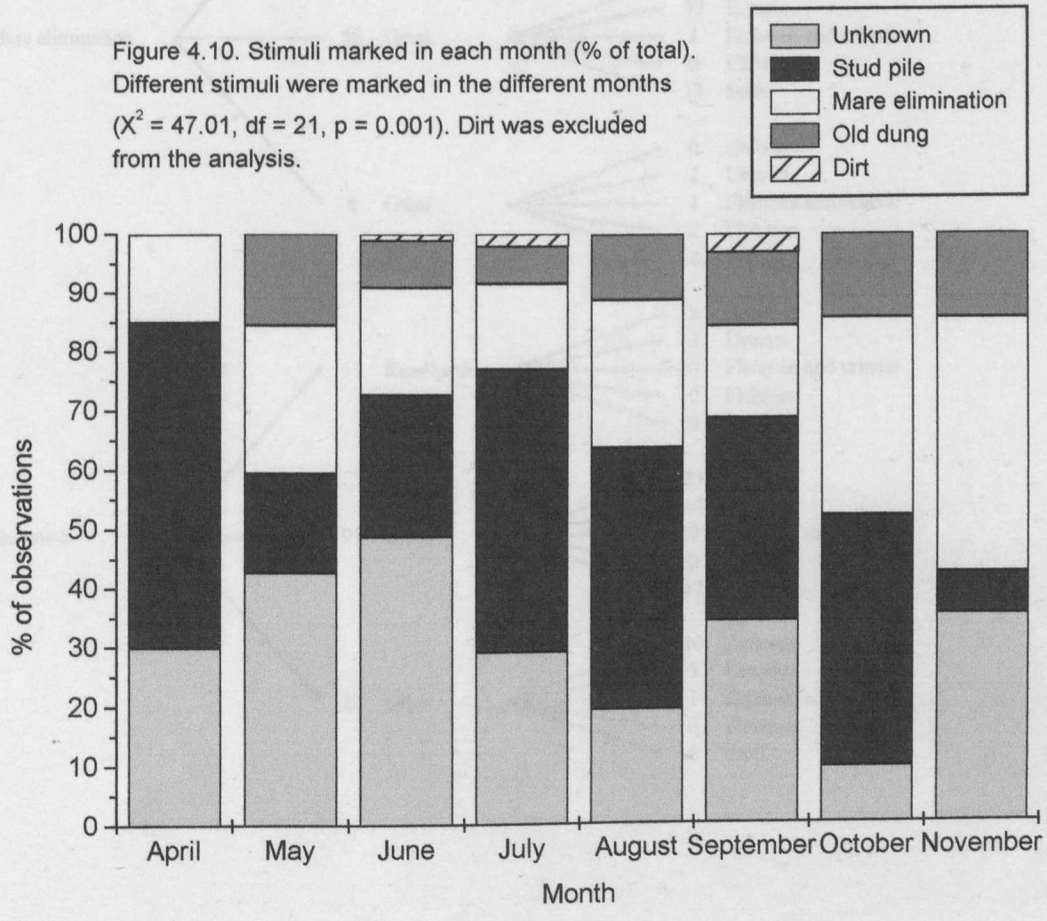
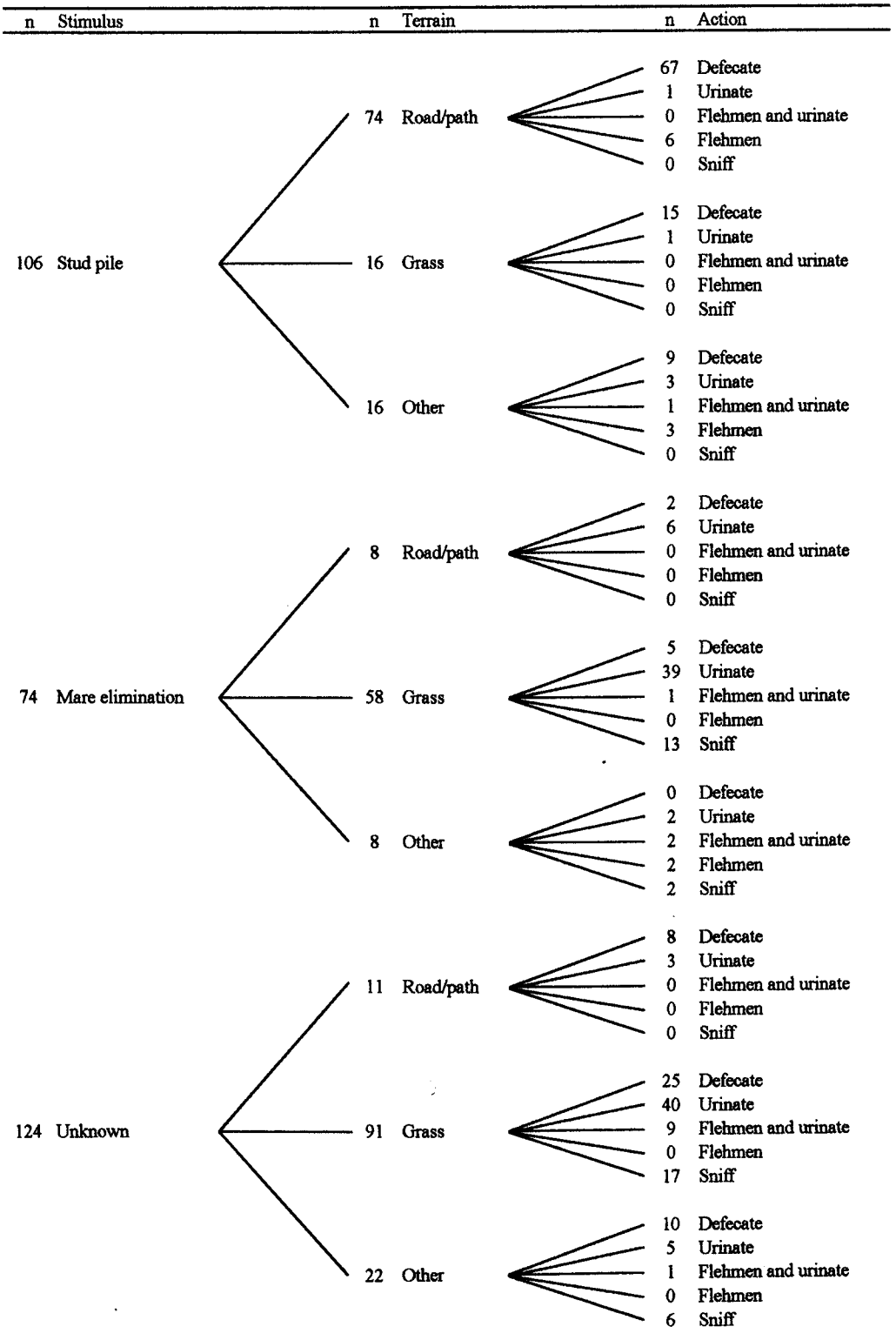


Figure 4.11. Pattern of marking behaviour.



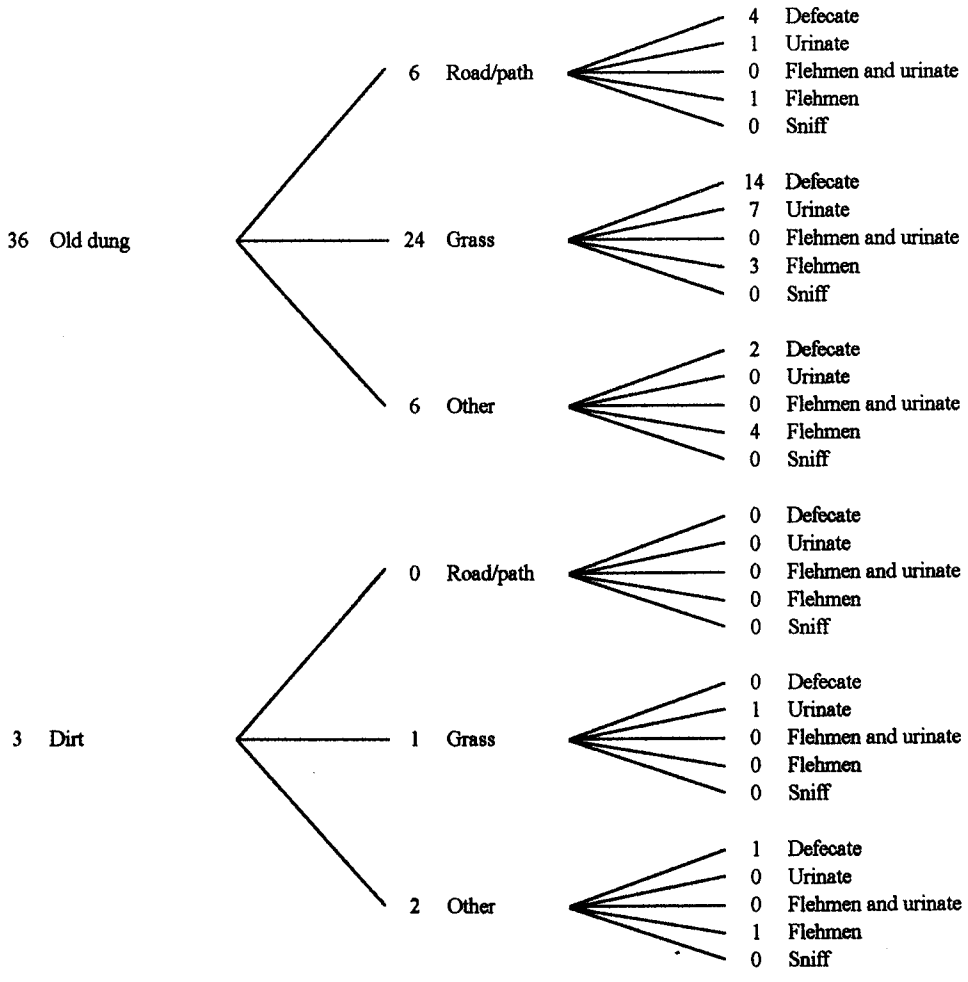

36 Old dung
6 Road/path
4 Defecate
1 Urinate
0 Flehmen and urinate
1 Flehmen
0 Sniff
24 Grass
14 Defecate
7 Urinate
0 Flehmen and urinate
3 Flehmen
0 Sniff
6 Other
2 Defecate
0 Urinate
0 Flehmen and urinate
4 Flehmen
0 Sniff
3 Dirt
0 Road/path
0 Defecate
0 Urinate
0 Flehmen and urinate
0 Flehmen
0 Sniff
1 Grass
0 Defecate
1 Urinate
0 Flehmen and urinate
0 Flehmen
0 Sniff
2 Other
1 Defecate
0 Urinate
0 Flehmen and urinate
1 Flehmen
0 Sniff

Plate 4.1. Sequence of marking a stud pile.

a). The stallion (Margad) sniffs the stud pile.

b). The stud pile is walked over and marked with dung.

c). The stallion turns around and sniffs the stud pile again.

<0.0001; Table 4.13). It appears that the stallions tended to sniff before marking on mare eliminations (but not after), and would sniff both before and after marking stud piles. Just sniffing, no marking, occurred on 18% of mare eliminations and 19% of unknown stimuli. The frequency of only sniffing afterwards and not sniffing at all was too low to be included in the analysis.

Table 4.13. Sequence of behaviours when marking. Per cent of observed marking of each stimulus is shown.

	Sniff before	Sniff after	Sniff before and after	No sniffing
Stud pile	22	1	77	0
Mare elimination	84	1	13	1
Unknown	61	9	28	1
Old dung	43	5	52	0
Dirt	50	0	50	0

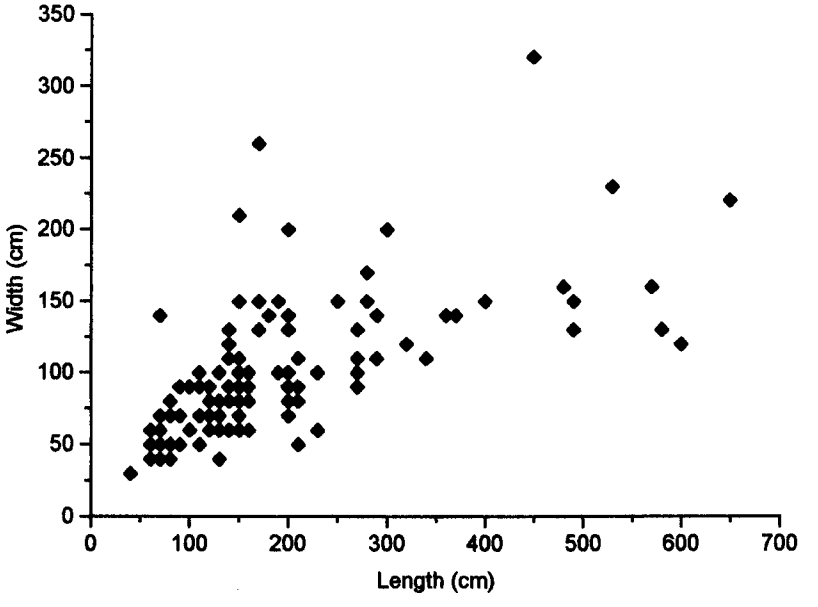
4.2.4.2 Stud piles

The dimensions of mapped stud piles are shown in Figure 4.12; the height is not shown but the median value was 5cm (IQR = 5cm –10cm). Predictably, stud piles that were used most frequently, i.e. new dung observed on an old stud pile, were also longer ($H = 30.89$, $df = 4$, $p = <0.0001$), wider ($H = 18.16$, $df = 4$, $p = 0.0011$) and higher ($H = 22.23$, $df = 4$, $p = 0.0002$) (Table 4.14).

Table 4.14. Median dimensions of stud piles of different ages (inter-quartile ranges are shown in brackets). The ages were based on the appearance of the dung.

Age	Length	Width	Height
New	85 (70.0-137.5)	65 (52.5-77.5)	10 (5.0-13.8)
Fresh on new	70 (55.0-85.0)	40 (37.5-102.5)	10 (5.0-16.3)
Fresh on old	140 (130.0-250.0)	90 (60.0-120.0)	10 (5.0-20.0)
New on old	200 (135.0-280.0)	110 (75.0-140.0)	10 (5.0-12.5)
Old	140 (102.5-182.5)	85 (70.0-125.0)	5 (5.0-5.0)

Figure 4.12. Dimensions of stud piles (cm) (n = 114). Median length was 145 cm (n = 114, IQR = 100-210) and median width was 90 cm (n = 114, IQR = 60-130).



There was no difference between the number of stud piles placed in the core or periphery of the home ranges ($X^2 = 7.50$, df = 4, p = 0.112, outside the home range was excluded from the analysis; Table 4.15 and Figures 4.13a to e). There was a tendency for more stud piles to be placed in areas where the home ranges overlapped ($X^2 = 19.64$, df = 4, p = 0.001).

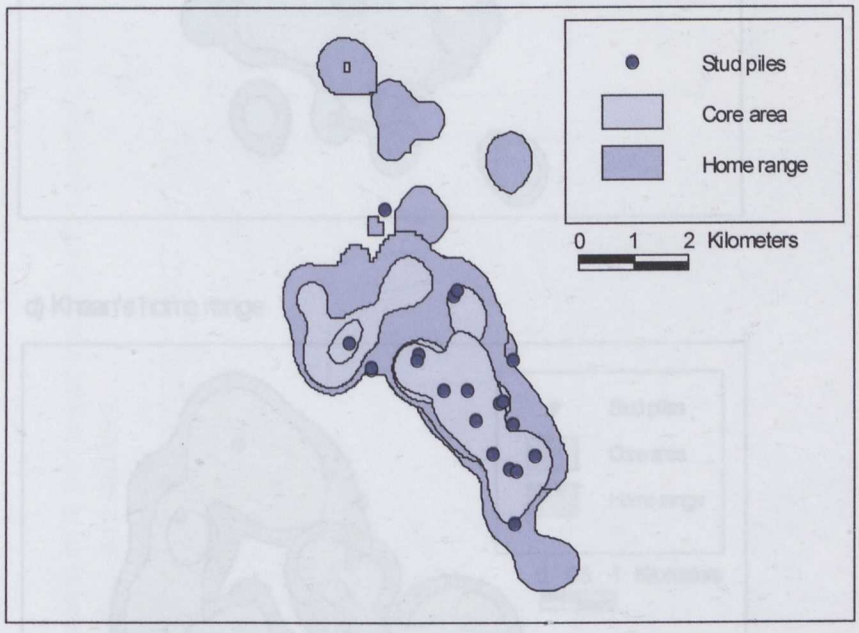
Table 4.15. Position of stud piles relative to the home ranges of the harems. Per cent of all mapped stud piles in each home range are shown.

Home range	n	Position relative to home range			Home range	Overlap
		Core area	Periphery	Outside		
Paritet	21	71	24	5	62	38
Bayan	15	80	7	13	0	100
Margad	7	57	43	0	42	58
Khaan	25	68	8	24	0	100
Ares	21	62	38	0	53	47

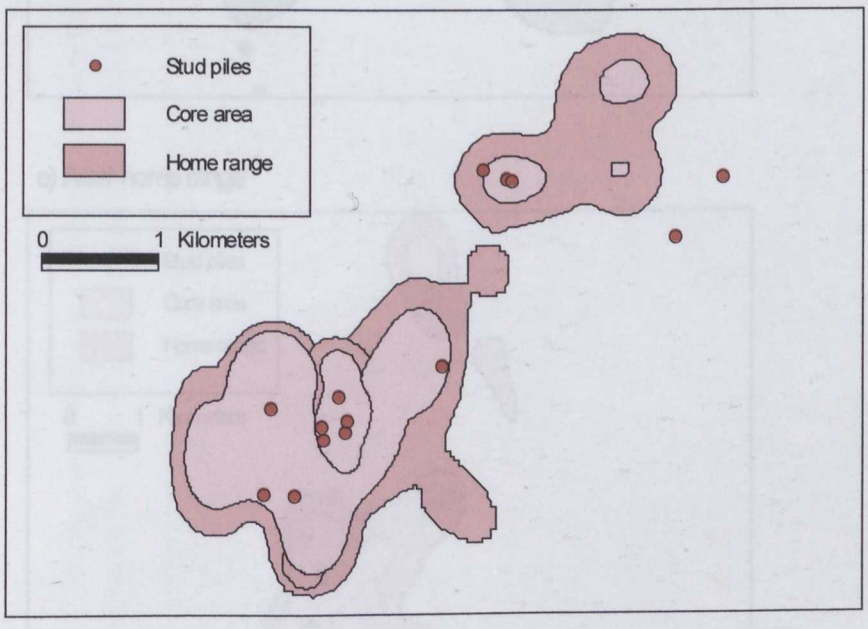
Figure 4.14 shows the situation of stud piles in relation to the landscape characteristics. Twenty five per cent of stud piles were found on ridges or saddles and most of the rest were found on paths or tracks as described before. It therefore appears that stud piles were placed where other stallions were most likely to come across them. There was a noticeable increase in the number of stud piles along a path used by

Figure 4.13. Position of all stud piles observed marked by the stallions and their home ranges (1998 and 1999 home ranges combined).

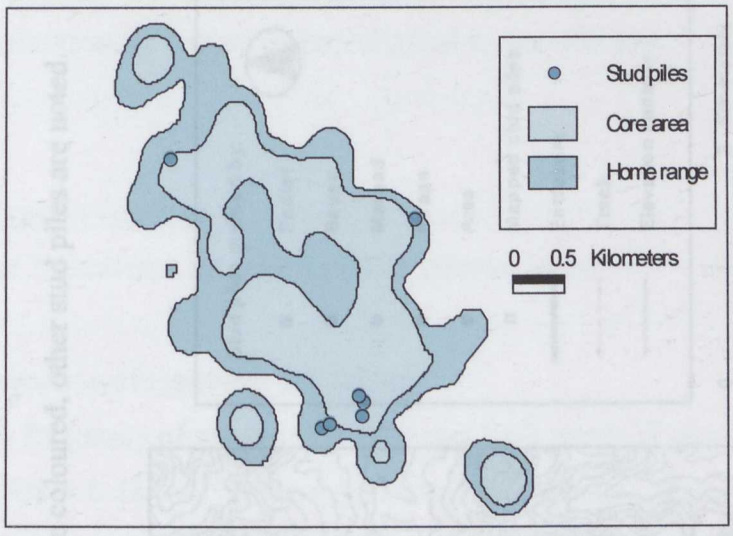
a) Paritet's home range



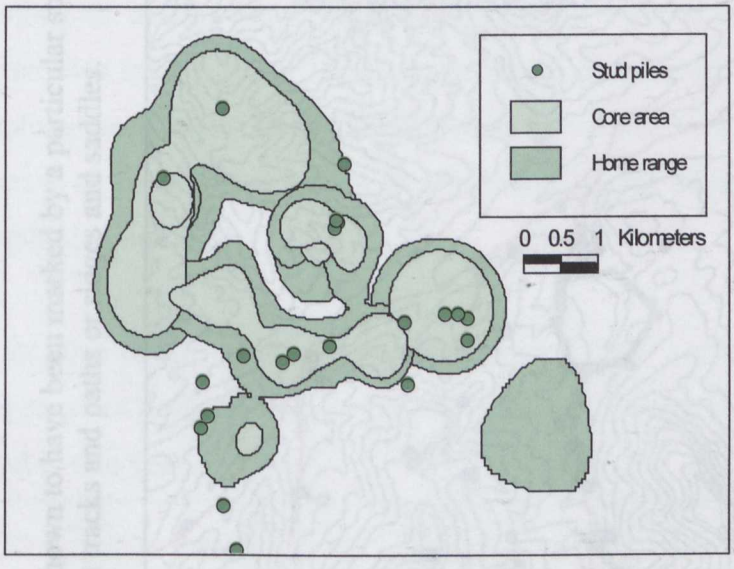
b) Bayan's home range



c) Margad's home range



d) Khaan's home range



e) Ares' home range

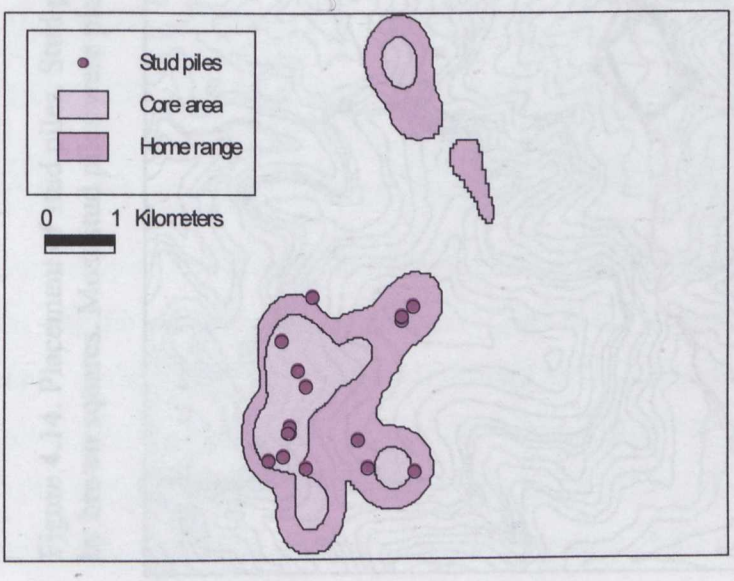
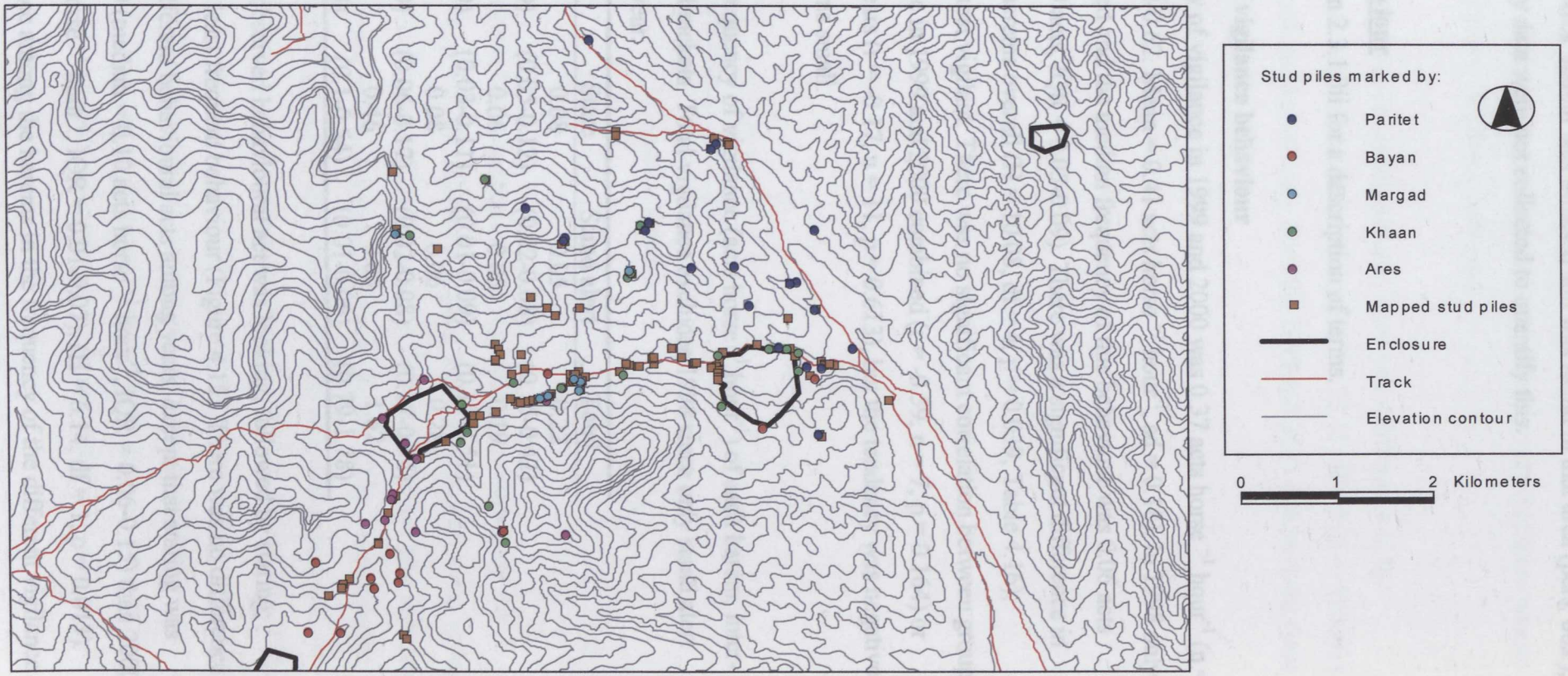


Figure 4.14. Placement of stud piles. Stud piles known to have been marked by a particular stallion are coloured, other stud piles are noted by brown squares. Most stud piles were placed on tracks and paths or ridges and saddles.



Khaan's harem after Ares' harem was released and was found in that area (pers. obs.), although unfortunately data were not collected to quantify this.

4.2.5 Vigilance behaviour

See Chapter 2, Section 2.3.1.3ii for a description of terms.

4.2.5.1 Frequency of vigilance behaviour

The median frequency of vigilance in 1999 and 2000 was 0.37 acts horse $^{-1}$ hour^{-1} (n = 2132 acts, IQR = 0.22-0.62. Mean = 0.41 acts horse $^{-1}$ hour^{-1}, sd = 0.18). In 1998 only stand alert was sampled and the median frequency of this behaviour was 0.06 acts horse $^{-1}$ hour^{-1} (n = 83 acts, IQR = 0.05-0.09). There was a significant difference in vigilance among the harems overall ($H = 10.08$, $df = 4$, $p = 0.039$; Table 4.16); Khaan's harem was most vigilant. There was no significant correlation between group size and total vigilance in 1999 and 2000 combined ($r = -0.59$, $n = 7$, $p = 0.164$) or standing alert in all years ($r = -0.17$, $n = 11$, $p = 0.613$), but the tendency was negative and the sample size was small.

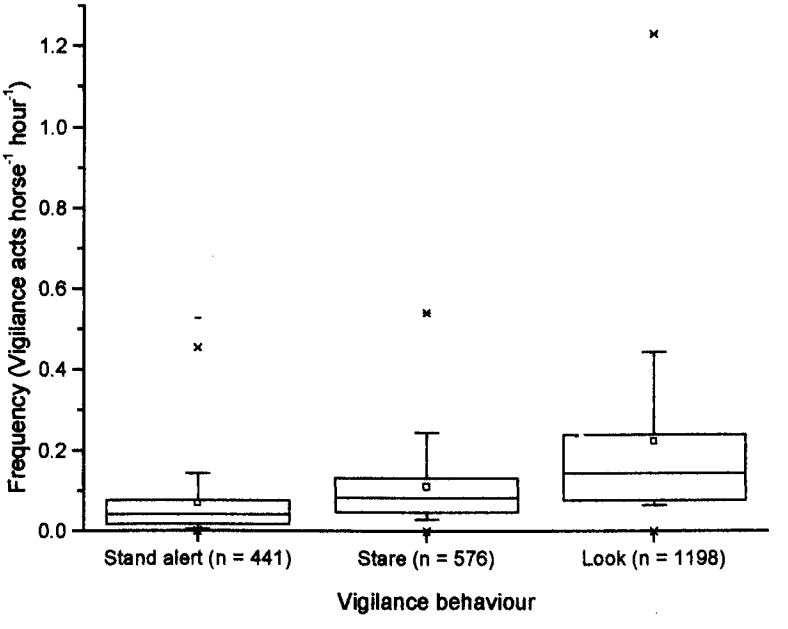
Table 4.16. Median frequency of vigilance (acts horse $^{-1}$ hour^{-1}) of each harem, inter-quartile ranges are in brackets. Total vigilance excludes 1998 since only stand alert was observed in that year.

	Look	Stare	Stand alert	Total
Paritet	0.17	0.08	0.05	0.22
	(0.08-0.40)	(0.05-0.12)	(0.02-0.08)	(0.15-0.42)
Bayan	0.10	0.06	0.05	0.19
	(0.07-0.20)	(0.03-0.11)	(0.01-0.09)	(0.13-0.51)
Margad	0.12	0.08	0.06	0.28
	(0.09-0.20)	(0.06-0.17)	(0.02-0.08)	(0.17-0.52)
Khaan	1.11	0.46	0.05	1.62
	(0.23-1.23)	(0.1-0.54)	(0.01-0.06)	(0.79-1.78)

The most frequently observed behavioural act was looking, followed by staring; standing alert was the least frequent behaviour (Figure 4.15). There was no difference in the frequency of different behavioural acts among years, except that staring was more frequent in 1999 (median = 0.10 acts horse $^{-1}$ hour^{-1}, IQR = 0.06-0.15) than 2000 (median = 0.06 acts horse $^{-1}$ hour^{-1}, IQR = 0.01-0.07), ($H = 6.14$, $df = 1$, $p = 0.013$). There was no difference among the harems in the frequency of the different vigilance

behavioural acts (look - H = 6.17, df = 3, p = 0.104; stare - H = 6.94, df = 3, p = 0.074; stand alert - H = 3.13, df = 3, p = 0.371). It therefore appears that there was no effect of time since release on vigilance behaviour.

Figure 4.15. Frequency of vigilance behaviours. There was a difference in the frequency at which these behaviours were expressed (H = 23.11, df = 2, p = <0.0001). Values for stare and look are derived only from the 1999 and 2000 data because these behaviours were not sampled in 1998.

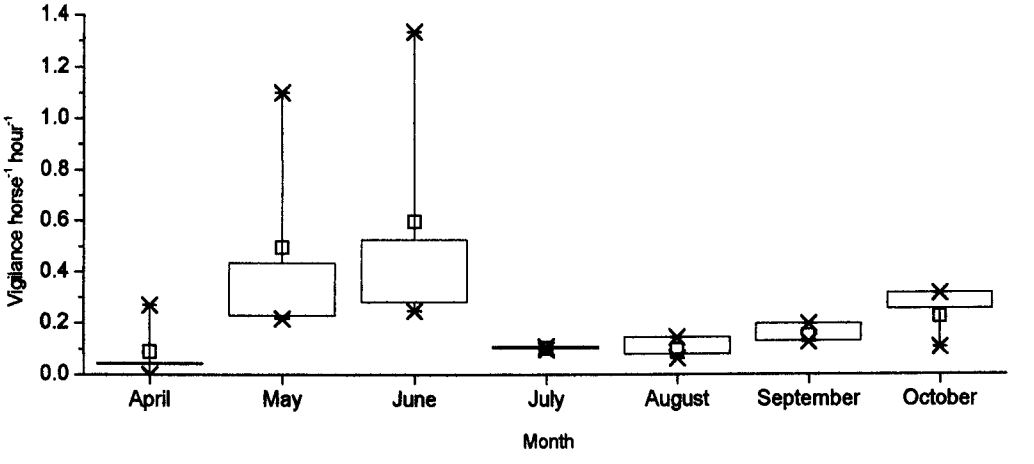


There was no difference in the frequency of total vigilance observed among the months (H = 9.83, df = 6, p = 0.132). However a trend for more vigilance in the spring (May and June) and the late autumn (October) than in the rest of the year was apparent when the different vigilance behaviours were examined (Figure 4.16). These months cover the foaling and breeding season, and when most foals were lost to wolves.

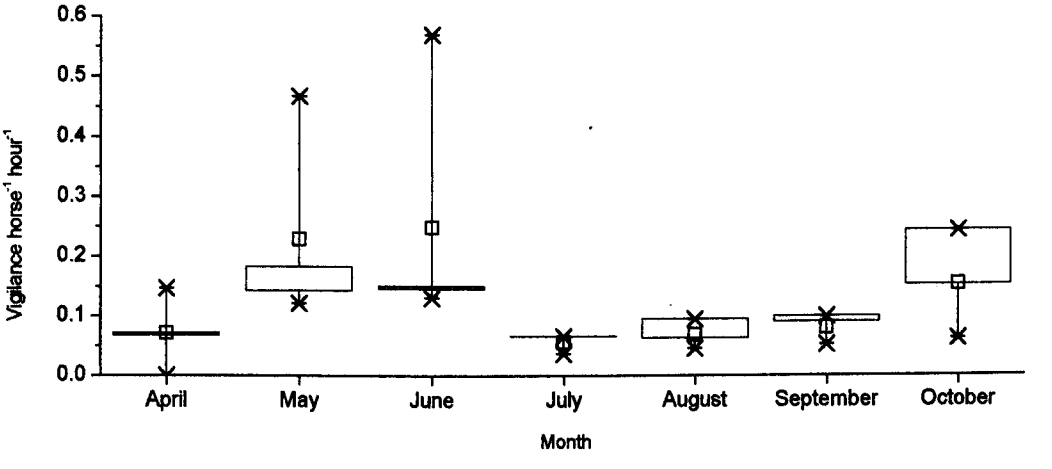
Less vigilance overall was observed in the early morning (0500-0600), middle of the day (1200-1300) and in the evening (1800-2000) than through the rest of the day (H = 78.50, df = 15, p = <0.0001), although this tendency varied with the different behaviours (Figure 4.17). There was a difference among the harems as Khaan and Ares were not significantly more vigilant at certain times of the day (H = 48.87, df = 4, p = <0.0001).

Figure 4.16. Box plots to show the frequency of vigilance in each month. Results for look and stare are from 1999, the stand alert results are from 1998 and 1999 combined (data from 2000 were not used as they only covered May and June). Most looking (H = 14.70, df = 6, p = 0.023) and staring (H = 12.54, df = 6, p = 0.05) occurred in May, June and October. There was no significant difference in the frequency of stand alert according to month (H = 0.68, df = 6, p = 0.995).

a) Look



b) Stare



c) Stand alert

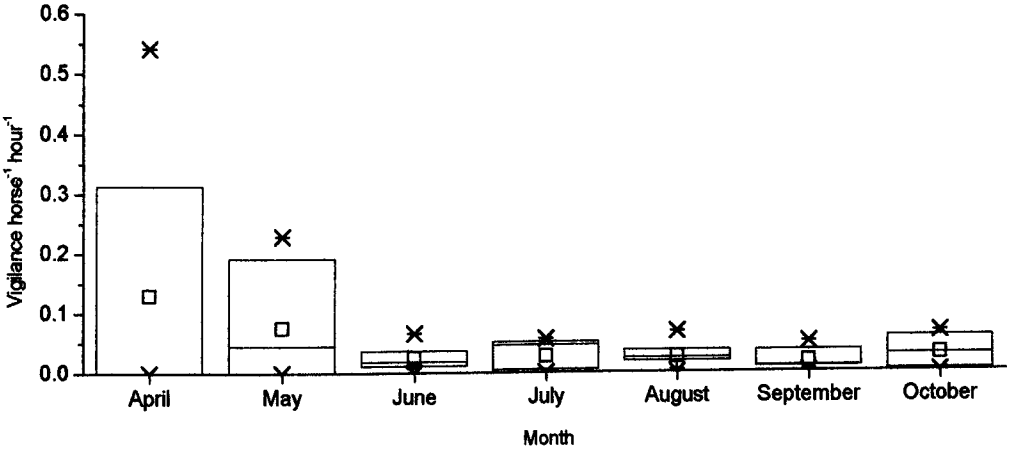
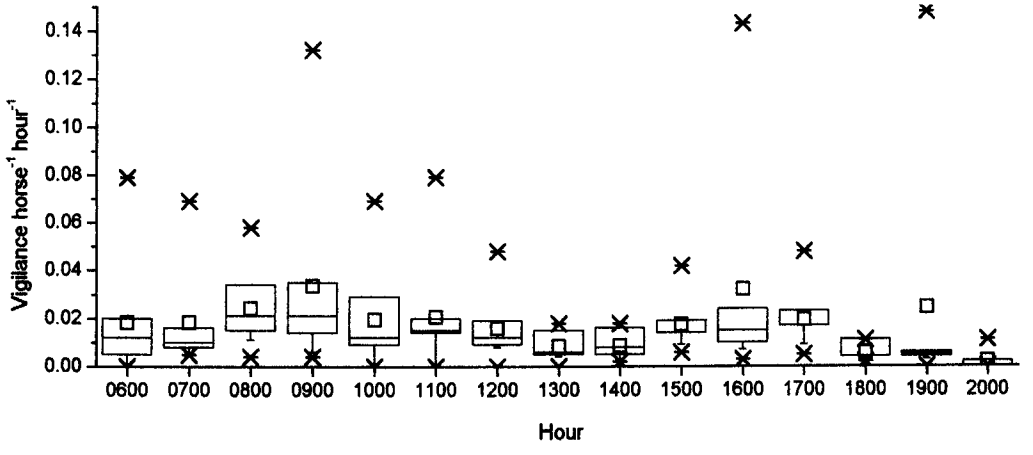
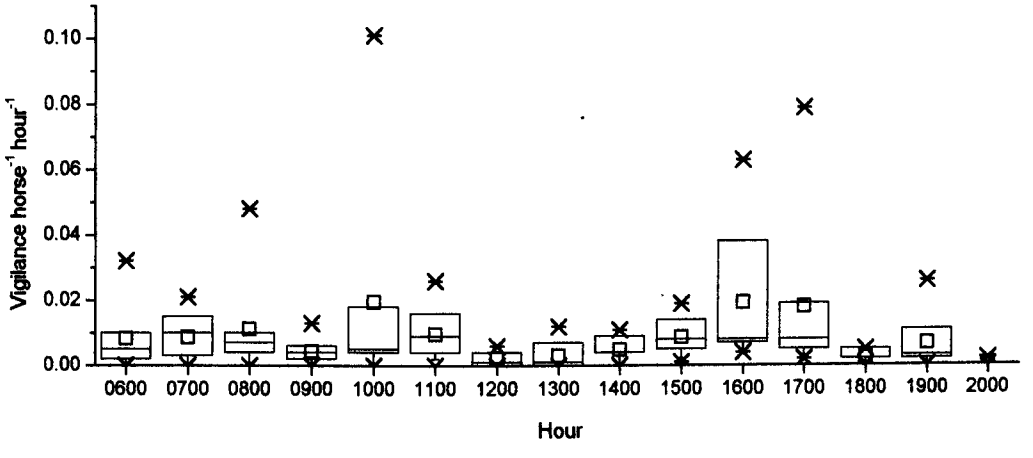


Figure 4.17. Box plot to show the frequency of vigilance across the hours of the day. Data shown are for all years combined. There was no significant difference among the hours for staring (H=24.49, df=15, p=0.0573) or standing alert (H=18.12, df=15, p=0.2563). More looking was seen in some hours (H=44.17, df=15, p=0.0001).

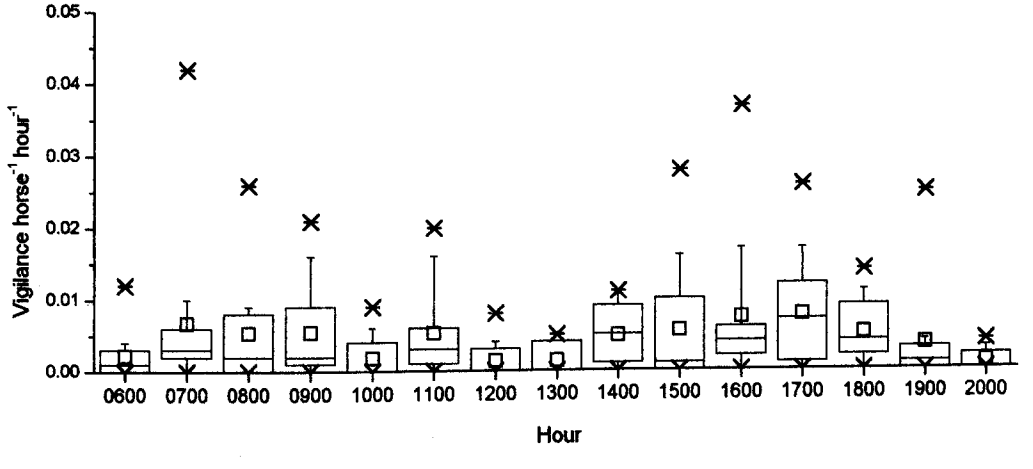
a) Look



b) Stare



c) Stand alert



4.2.5.2 Vigilance according to age and sex

Overall the stallions were most vigilant, followed by the mares then the juveniles (X^2 = 163.66, df = 2, p = <0.0001; Table 4.17). Vigilance by foals was not recorded. There was no difference among the ages and sexes in the tendency to look more than stare or stand alert (X^2 = 6.72, df = 4, p = 0.151).

Table 4.17. Vigilance of each age and sex (% of total, justified for number of horses, excluding 1998).

	n	Look	Stare	Stand alert	Total
Stallion	661	46	64	67	57
Mare	1183	30	26	24	27
Juvenile	234	24	13	9	16

On 37 occasions through the entire study period the whole harem was observed to become vigilant at the same time. There was no difference between the harems in the frequency of all becoming vigilant (H = 1.95, df = 3, p = 0.583), and they did not tend to exhibit any particular behaviour when they were all vigilant (H = 1.95, df = 3, p = 0.583).

4.2.5.3 Stimuli causing vigilance

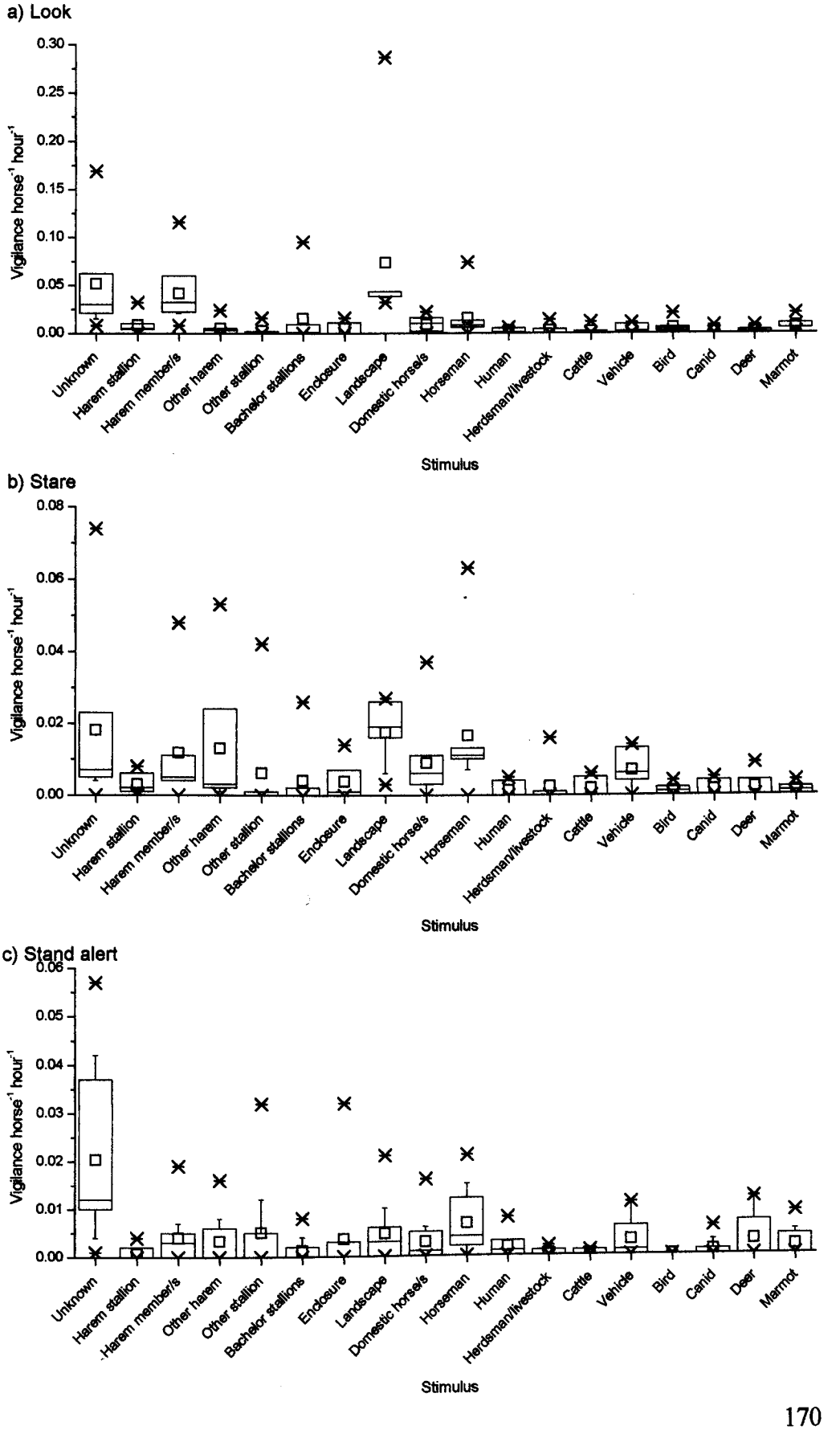
The stimuli of most vigilance overall were unknown, harem members, the landscape and the harem stallion (X^2 = 2804.08, df = 20, p = <0.0001), these stimuli also accounted for most looking (Figure 4.18a). Most staring was at unknown, the landscape and horsemen (Figure 4.18b), and the main stimulus causing the horses to stand alert was unknown (Figure 4.18c).

There was a difference in stimuli causing the different harems to become vigilant (H = 17.93, df = 4, p = 0.0013). Paritet's harem had a higher incidence of vigilance towards domestic horses and horsemen and Margad's harem towards strange harems than the other harems. Bayan's and Khaan's harems were vigilant towards a less wide range of stimuli than Paritet and Margad's.

4.2.5.4 Vigilance of individual horses

Spearman's rank correlation was used to examine associations among factors affecting the mean value of vigilance of each horse. There was a significant but weak positive correlation between vigilance and aggression hour^{-1}, age and tenure, and a negative

Figure 4.18. Stimuli causing vigilance (vigilance/min) (+1 se). Certain stimuli caused the horses to a) look (X^2 = 1867.11, df = 17, p = <0.001), b) stare (X^2 = 316.75, df = 17, p = <0.0001), and c) stand alert (X^2 = 361.15, df = 17, p = <0.0001) more than others. There was no difference in these stimuli among the years (look - H=1.25, df=1, p=0.2637; stare - H=2.24, df=1, p=0.1341; stand alert - H=0.39, df=2, p=0.8229).



correlation between vigilance and rank (Table 4.18). There was no difference between the vigilance of mares with foals, and mares of the same age and similar rank without a foal (paired t = 0.07, df = 35, p = 0.95).

Table 4.18. Spearman's rank correlation of various factors affecting vigilance. Aggression is the number of acts horse $^{-1}$ hour^{-1}.

Factor	r_s	p
Dominance rank	-0.34	0.0005
Aggression	0.41	<0.0001
Age	0.34	0.0006
Tenure	0.28	0.0058

In 1998, when only standing alert was recorded, there was no difference in the vigilance among the individual horses within each harem (Paritet – H = 4.0, df = 6, p = 0.677; Bayan – H = 6.34, df = 5, p = 0.274; Khaan – H = 11.06, df = 13, p = 0.606). In 1999 there was no difference in the vigilance among the horses in Bayan's (H = 14.01, df = 7, p = 0.05) or Khaan's harems (H = 11.43, df = 6, p = 0.076). However in Paritet's and Margad's harem there was a strong difference among the horses (H = 66.54, df = 10, p = <0.0001 and H = 53.04, df = 13, p = <0.0001 respectively). In both cases the stallion was the most vigilant individual. In Paritet's harem Ayunga, a mare that joined the harem in 1999, was more vigilant than most of the other mares and the juveniles were less vigilant. The mare Uvul was less vigilant than any other horse in the harem. In Margad's harem the least vigilant horses were Svetlaya and the juvenile Selenge. Horses that were only in the harem for a short time also had very low vigilance (e.g. Delgerekh and Zigmee). In 2000 there was no difference among the horses within any harem except for Paritet's harem (Paritet – H = 28.57, df = 13, p = 0.008; Bayan – H = 15.11, df = 8, p = 0.057; Margad – H = 18.91, df = 11, p = 0.063). Again, Paritet was more vigilant than any of his mares, and Naidvar and Buyana were the most vigilant mares. Tengis' yearling was significantly less vigilant than most of the other horses in the harem.

4.3 DISCUSSION

4.3.1 Agonistic behaviour

Many papers have been published on agonistic behaviour in horses, but relatively few state the frequency with which aggressive acts were observed. Comparison is also made difficult by different authors using different behaviours by which they define aggression. However, as this study used all aggressive behavioural elements to calculate the frequency of aggression it is likely that almost all agonistic behaviour was accounted for, whereas other studies are more likely to produce a lower frequency if they only use certain behaviours. Thus it can be seen that the frequency of aggression of the Przewalski horses at HNP (mean = 0.35 acts hour^{-1}) was much lower than that reported in other populations of horses. Feral horses at Assateague were observed to have a frequency of 1.3 acts hour^{-1} (Houpt & Keiper, 1982), and then 2.4 acts hour^{-1} four years later (Keiper & Sambraus, 1986). Other populations of feral horses have been reported to have both lower (1.9 acts hour^{-1} among highland ponies (Clutton-Brock *et al.*, 1976)) and higher (3.5 acts hour^{-1} in the Camargue (Wells & von Goldschmidt-Rothschild, 1979)) frequencies than this latter figure. A group of three to seven Przewalski horses in a zoo aggressed at a frequency of 0.9 ± 1.1 acts hour^{-1} (Kolter & Zimmermann, 1988), and in reserves, frequencies as high as 10.4 acts hour^{-1} have been observed (in a harem of seven horses) (Keiper & Receveur, 1992).

The low frequency of aggression among the horses at HNP is likely to have been influenced by two factors: the horses were unconfined and they had been together for several years. All of the horses in the studies quoting high frequencies of vigilance were confined in some sense, either by the boundaries of an island or else by a fence. Horses had a lower frequency of aggression when released into a large paddock than when in small enclosures (Hogan *et al.*, 1988). Even when large areas are available to horses it is possible that the presence of a boundary has an effect on their reaction to each other. Most studies of dominance in domestic horses have used paired feeding trials examining which animal gains access to food (Ellard & Crowell-Davis, 1989; Houpt *et al.*, 1978; Houpt & Wolski, 1980). Studies of feral horses also frequently used access to limited resources, such as water holes, to assess inter- and intra-harem dominance (Berger, 1977; McCort, 1984; Miller & Deniston, 1979); most aggression will be observed when there is direct competition between horses. In HNP there were few instances where resources were only available to one horse at a time, which could

be cause for conflict, and there was always room for a horse to move away from a confrontation. The harems were all well established and besides the occasional dispersal between harems, the main additions were births. Therefore it is likely that the horses were aware of the fighting ability and position in the hierarchy of each other horse, and so were able to form an appropriate response to any threat (Clutton-Brock *et al.*, 1982; Franke Stevens, 1988).

The same behavioural elements have been observed in aggressive situations in all populations of equids, enabling lists of behaviours to be formed (Moehlman (1998) for feral asses, McDonnell and Haviland (1995) for domestic bachelor stallions, and Boyd and Houpt (1994) for Przewalski horses). These same behaviours were observed in the Przewalski horses at HNP and similar behaviours were most common in this population as in others. A tendency for aggression to be more frequent in larger groups, independently of the amount of time horses spend close together has been reported from other studies (McCort, 1984; Rutberg & Greenberg, 1990). Individuals in larger groups possibly have to compete more for the best resources resulting in more aggression, or simply come into contact more often. Although this was not seen here, the situation may change as the population grows.

There are some behaviours that are typically conducted by the stallion, such as herding, and in the Przewalski horses in Munich Zoo 40% of all aggression consisted of herding by the stallion (Keiper, 1988). This was the main behavioural element observed in the stallions at HNP, and they had a higher frequency of aggression than the mares largely because of the high incidence of this behaviour. The behavioural elements observed in the mares were also similar to those seen in other studies (e.g. Keiper and Receveur (1992); Weeks *et al.* (2000)). There was no difference between the behaviour of Khaan's harem and Margad's showing that the aggression expressed by the mares was not affected by the change in stallion.

Several studies have separated offensive from defensive behavioural elements (van Dierendonck *et al.*, 1995; Wells & von Goldschmidt-Rothschild, 1979), and stated that only the offensive behaviours should be used to form a dominance hierarchy (van Dierendonck *et al.*, 1995). In this study defensive behaviour was very rare, although, besides moving, the horses did use hind leg kick as a defensive or retaliatory behaviour. More hind leg kick was used as an aggressive behavioural element directed up the hierarchy than down, but in each case it was used as an aggressive behaviour, instigated by the lower ranking horse, not simply as a defence. There is therefore little

evidence that the behavioural elements should be used differently to form a hierarchy in this population.

Aggression primarily in one direction enables the formation of a hierarchy, so it was expected that most aggression would be directed down the hierarchy at HNP. Ellard and Crowell-Davis (1989) found most aggression between horses of a similar rank, but at HNP very little aggression was directed at the animal immediately above or below it in dominance rank. The presence of a hierarchy would result in dominant animals receiving least aggression, but the aim of an aggressive act was unlikely to be simply to raise an animals position by one place in the hierarchy, as has previously been hypothesised (Ellard & Crowell-Davis, 1989), but for other reasons such as direct competition for resources.

Mares and juveniles received more aggression than the stallions, and this would have affected their relative positions in the dominance hierarchy. The stallion was dominant in all harems in all years, except for Bayan's in 1998 and 1999. In other studies the stallion has not always been the most dominant animal in the harem (Houpt & Keiper, 1982; Keiper & Sambraus, 1986). Stallions have been recorded to be dominated by older or well established mares (Keiper & Sambraus, 1986; Kolter & Zimmermann, 1988), or be apparently least dominant in the hierarchy as they take part in few interactions and spend more time at the periphery of the harem (Keiper & Sambraus, 1986). In the case of Bayan's harem it is likely that more data were needed to form a better view of the dominance hierarchy, because aggression was rare in this harem. Juveniles were normally subordinate to adults, as in other studies (Houpt *et al.*, 1978).

This study used a very rigorous method to form the hierarchy of the harems (de Vries & Appleby, 2000). Most other studies simply divided aggressive acts (or supplants) won, by those that were lost. This will produce a different rank order of the horses. Although the accuracy of the hierarchy will depend on the amount of data obtained (interactions between all pairs will provide a clearer view of relative dominance), the validity of the ultimate rank order will also be tempered by knowledge of the animals from the field. Although signals can be very subtle, Bayan did not appear to be dominated by his mares in 1998 or 1999, and proved to be dominant in 2000.

The lack of significant linearity in the hierarchy of some harems in some years means that the rank order is unlikely to be totally accurate, but is a useful guideline. Inconsistencies were only found in Bayan's harem, so the non-linearity of the hierarchies were unlikely to be because of triangular relationships, but could be due to

unknown relationships between pairs and the relatively small data set. Houpt *et al.* (1978) found triangular relationships in large harems of domestic horses in paddocks, whereas the smaller harems had a linear hierarchy. There was no evidence of this here as one of the smallest harems had the triangular relationship and the largest was linear.

The hierarchies appeared to be quite stable from one year to the next with only a few changes among the mares. The most noticeable changes in rank were for horses that newly joined a harem. In the first year they were with the harem they received a lot of aggression and were low ranking, even below juveniles, in all cases. In the following year they had improved their position. The mare Delgerekh even attained a higher position than some of the original, established mares a year after having joined Bayan's harem. Dispersing mares often received more aggression in a new harem than they did before dispersal (Monard & Duncan, 1996; Rutberg, 1990), so it is hypothesised that they gain greater benefits by leaving than they lose from costs of receiving aggression. In the case of the dispersing adult mares at HNP it is hard to see what these costs and benefits were. Unlike other studies, Rutberg and Greenberg (1990) found no difference in aggression between mares that had changed harems and those that were resident.

Height and weight have been reported as two of the main determinants of dominance (Ellard & Crowell-Davis, 1989; Houpt *et al.*, 1978; Rutberg & Greenberg, 1990; Tyler, 1972), though not in all populations (van Dierendonck *et al.*, 1995; Feh, 1990). Unfortunately it was not possible to measure these parameters at HNP. However age, which is related to size, was known for all animals and older animals tended to be dominant over younger, as reported in most studies (van Dierendonck *et al.*, 1995; Ellard & Crowell-Davis, 1989; Keiper & Receveur, 1992; Keiper, 1988; Keiper & Sambraus, 1986; Rutberg & Greenberg, 1990; Tyler, 1972; Wells & von Goldschmidt-Rothschild, 1979), with the exception of Houpt *et al.* (1978). Related to this was the fact that horses which had spent longer in a harem were dominant over immigrants or younger horses, as seen in Iceland (van Dierendonck *et al.*, 1995). Tyler (1972) found that aggression was a major determinant of dominance as a very aggressive mare was high in the hierarchy even though she was relatively small and young. This study, and Ellard and Crowell-Davis (1989), Houpt *et al.*, (1978) and Weeks *et al.* (2000) also found a tendency for more aggressive horses to have a higher position in the hierarchy, but aggression also positively correlated with age so it is uncertain which of these factors were more important.

The presence of a hierarchy will act to keep the group together. Although young horses may have fewer costs in moving to a new harem, once a mare is established in a harem she is likely to lose the benefits of her higher ranking if she moves. A dominance hierarchy was evident in all harems at HNP, although more work would be useful to examine the linearity of the hierarchies and their stability over a greater time scale. The dominance hierarchies appear to be structured and maintained in a similar way to other horse populations. It is hard to quantify what horses at HNP gain by being more dominant as the resources were widely dispersed, with the exception of shading places in the summer. This possibly accounts for the low aggression that was seen in this population and means that dominance is unlikely to directly affect the mortality of individuals, and so act to regulate the population, as was found in dominant roe deer and reindeer, which were able to monopolise scarce winter resources (Espmark, 1974). As the population grows, inter-harem/stallion dominance ranks may have more of an impact, especially if home ranges overlap at water sources or resting places.

4.3.2 Associative social behaviour

Associative behaviours were rare among the horses at HNP, occurring much less frequently than aggression. Other studies also found that these behaviours were rare (Carson & Wood-Gush, 1983a; Wells & von Goldschmidt-Rothschild, 1979), but mutual grooming was ten times less frequent at HNP than among Przewalski horses at San Diego Wild Animal Park (Mooring *et al.*, 2000). Only one study found non-aggressive behaviours were more common than aggressive (Keiper & Receveur, 1992), but they included nursing behaviour which will have affected the results. More mutual grooming was found in smaller enclosures than on a pasture (Hogan *et al.*, 1988; Keiper & Receveur, 1992), which may also have been the cause of the more frequent non-aggressive behaviours observed in the group in a reserve by Keiper and Receveur (1992). Hogan *et al.* (1988) hypothesised that the constant proximity of horses within the small enclosure, and the lack of other stimuli, increased the probability of mutual grooming, as well as aggression, among them. An extension of this hypothesis would be that horses without limits to their movements and no lack of stimuli would only mutual groom (or aggress) as much as was defined by the social structure of the harem, or as necessary to remove loose hair and parasites.

It would be expected that related animals would spend more time together and so more mutual grooming and other associative behaviours would occur between them. However, although this was found in the Munich Zoo (Keiper, 1988), it was not found in HNP or by Clutton-Brock *et al.* (1976) in highland ponies, or Mooring and Hart (1995) in impala. Some studies found that most associative behaviours occurred between horses that spent most time together (Carson & Wood-Gush, 1983a; Clutton-Brock *et al.*, 1976; Feh, 1999; Kimura, 1998), and that they tended to have preferred partners. Exceptions to this are the population of mountain zebras in the Mountain Zebra National Park that had no preferred partners (Penzhorn, 1984), and no mutual grooming at all was observed in Cape or Hartmann's Mountain zebras by Klingel (1968) (in Feist (1971)).

Most interactions occurred between mares and juveniles at HNP, although mare – mare and mare – stallion interactions were also frequent. As mares and their offspring were often close together this is to be expected. The frequency of interactions between ages and sexes has been reported to vary in other studies. Crowell-Davis *et al.* (1986) observed little mutual grooming by or among adult horses and nearly half of all mutual grooming observed by Keiper (1988) was by foals. When studying Przewalski horses in a reserve however, Keiper and Receveur (1992) found most mutual grooming was initiated by mares.

The withers were groomed more than any other body part. It was this region that Feh and de Mazieres (1993) found was associated with a reduced heart rate in horses and so hypothesised that it acted to reduce tension. There was no correlation between aggression and frequency of mutual grooming at HNP (or in highland ponies (Clutton-Brock *et al.*, 1976)) and there was no direct evidence that mutual grooming reduced tension among the horses. However as most mutual grooming occurred between mares and juveniles its function as weaning appeasement cannot be ruled out. There was also no correlation between length of time in a harem, age or rank and frequency of mutual grooming. One other study also found no correlation between theses factors (Clutton-Brock *et al.*, 1976), but others found a correlation between mutual grooming frequency and aggression (Feh & Carton de Graumont, 1995), age (Keiper & Receveur, 1992; Keiper, 1988), and rank (Keiper & Receveur, 1992; Keiper, 1988).

Most mutual grooming occurred in the spring, when ticks were abundant, and autumn, when the horses were moulting. This implies a hygiene function of mutual grooming and that it was stimulus driven, rather than a programmed response

(Mooring *et al.*, 2000). Horses cannot reach areas of their back and tail to scratch or remove hair except by rolling, so mutual grooming is important for this. (Kimura, 1998) observed most mutual grooming in the summer, and thought that it was not more common during moulting times because crows removed loose hair. Although magpies were observed perching on Przewalski horses (pers. obs.) it appears they did not reduce the need for mutual grooming. It is unlikely that mutual grooming has absolutely no social function and is purely for hygiene as it always occurred reciprocally between horses, although this could be to prevent cheating and is simply an example of evolved cooperation (Mooring & Hart, 1995). Crowell-Davis *et al.* (1986) felt that mutual grooming between females promoted bonding between horses and so acted as a basis for cohesiveness of a harem independently of the stallion. Most mutual grooming occurred in the morning and evenings, when the horses were most active, suggesting that it is possible that it does occur to bond together members of the harem. However a function of mutual grooming other than to remove hair and parasites could not be quantified here.

Stand resting together enables horses to keep flies away by whisking their tails around the head of a partner, thus it tended to be most frequent during the summer and/or the middle hours of the day, when flies were most active. Nearest neighbour data were not gathered in this study, but stand resting together reflects these associations among the horses. Aggression occurred more often when horses were in an enclosed area as the increased proximity increased the likelihood of interactions (Hogan *et al.*, 1988), but this is because horses do not allow all other individuals to come close to them. Stand resting together would therefore only occur between pairs of horses that allowed each other into their 'personal space'. Surprisingly there were no correlations between stand resting together and relatedness or length of time in the harem, or other factors, as for mutual grooming, but it is possible that this is due to the small sample size since both of these behaviours were rare.

The function of mutual grooming has been much discussed in the literature. This study showed no evidence of a social function of either mutual grooming or stand resting together, but both occurred most frequently at times of year when they would be needed for coat care or to attempt to reduce the number of flies around the face. A social element of the behaviours cannot be ruled out as the sample size was small (due to the rarity of the behaviours) and further work might be rewarding.

4.3.3 Marking behaviour

The stallions at HNP marked mare eliminations and formed dung piles as in most other equid populations (e.g. Turner *et al.* (1981)). Typical postures were adopted by the stallions when marking, as described by Feist and McCullough (1976), Rubenstein and Hack (1992), Salter and Hudson (1982) and Turner *et al.* (1981). Although the same ritualised postures were observed when both stud piles and mare eliminations were marked, they were marked in different ways. Stud piles were marked with dung, and were sniffed both before and after they were marked, whereas mare eliminations were marked with urine and only sniffed before marking. This suggests that marking the two stimuli had different functions. The two stimuli were also found in different places suggesting that they will have a different impact on another animal encountering the mark. Mare eliminations were normally on grass, as that is where the mares spent most of their time, but stud piles were found on roads or ridges and stallions would move to a stud pile to mark it, as well as when they passed one in their daily movements.

There was no evidence that stud piles were used to mark the boundaries of the home ranges, as they occurred throughout the stallion's range. Instead, as Rubenstein and Hack (1992) found that dung contained information on the identity of a stallion, stud piles could provide information of horses that have passed over ridges or along paths and thus show the spatial movements of other stallions as well as the occupier of the home range. This will allow harems to avoid each other, or choose to come into confrontation. In addition they may provide orientation points for a stallion (Salter & Hudson, 1982), and produce a familiar odour (Eisenberg & Kleiman, 1972) within his home range, which is possibly why the stud pile is sniffed after marking as well as before.

Although marking stud piles during confrontations was relatively rare in this study, marking will provide detailed information for the opponents, and may also act as some kind of release for aggressive behaviour (Turner *et al.*, 1981). In other situations the order in which the stud pile is marked has been reported to indicate the dominance hierarchy of the stallions or bachelors marking (Miller, 1981; Redman, 1996; Turner *et al.*, 1981). If stud piles act to separate the harems through space, and so reduce costly conflict between them, then their function is much more than the relict behaviour hypothesised by Klingel (1975).

It is most likely that the function of marking mare eliminations is to show associations between a stallion and mare (Turner *et al.*, 1981). Most of this marking occurred during the breeding season, when comparatively fewer stud piles, but more unknown stimuli were marked. These unknown stimuli were very likely to have been mare eliminations that were not observed being deposited as they were treated in the same way, and more marking of mare eliminations was observed in the breeding season by Turner *et al.* (1981), with few in the winter. However, even in the breeding season not all mare eliminations were marked, therefore it is unlikely that they were marked in an attempt to hide the scent, as suggested by Tyler (1972). The seasonal change in marking behaviour could be caused by changes in the pheromones present in the mare urine and dung (Turner *et al.*, 1981). Stimuli contained in mare eliminations, especially when detected by flehmen, has the potential to affect the sexual behaviour of animals (Eisenberg & Kleiman, 1972). Thus marking of mare eliminations, especially when the mare is in season, could provide information for all other horses that this stallion is her consort, and may also provide a sexual stimulus for the stallion.

It is likely that all stallions knew each other, and had an idea of their relative fighting potential (especially within the small population at HNP). If they can link the smell of a known stallion from a stud pile with the scent of the stallion's urine on an oestrus mare's urine, then they can assess the risks involved in attempting to either steal the mare or sneak a mating. Marking of mare eliminations may have evolved with the harem defence polygyny to benefit both the stallion associating with the mare and the mare. If the stallion is in good condition he will be less likely to be confronted and lose the mare, and the mare will not be harassed by a large number of stallions attempting to mate with her.

Some studies that have dealt with marking behaviour in horses have combined both the marking of stud piles and the marking of mare eliminations (e.g. Klingel (1972) and Salter and Hudson (1982)). As it appears that the two types of marking have very different functions it would be worthwhile for future work to focus on them separately.

4.3.4 Vigilance behaviour

Most studies of vigilance show a relation between group size and frequency of vigilance, which has led to the many eyes hypothesis (Elgar, 1989), but in this

population, and the Great Basin feral horse population (Berger, 1986), there was no evidence of this. However, the many eyes hypothesis also assumes that animals in larger groups are able to spend more time eating as they spend less time being vigilant and this was seen in this population (Chapter 3, Section 3.2.2.3). However Berger (1986) found that vigilance did not affect the feeding budget of the Great Basin horses. The lack of a correlation between vigilance and group size in this study may be due to the small sample size since vigilance was quite rare. As the population grows and more harems become available for study the relationship may become clearer. In other respects the horses followed the many eyes hypothesis as they scanned each other, possibly to determine their state of vigilance (Lima, 1995), and would become alert if the standing alert posture was maintained by another animal.

It was surprising that there were no effects of time since release on vigilance frequency, because newly released harems spent more time moving covering 'new' ground, and were likely to be under higher stress. However newer released harems spent more time resting than those that had been free ranging for several years. As animals need more rest when stressed, or when faced with difficult tasks (Dukas & Clark, 1995) the greater time spent resting could also reflect the greater vigilance of these horses, the effect of which was confounded by the small sample size. It is also possible that the horses were simply showing a basal level of vigilance for the species, as was seen in impala and wildebeest both before they suffered predation and in the population that had no predation threat, compared to those animals where predators were present (Hunter & Skinner, 1998).

The horses were more vigilant in the spring and autumn than at other times of the year, and it was in these periods that most foals were lost to wolves at HNP. In a population of feral horses on the Nevada/California border mountain lions limited the growth of the population and took most foals from May to mid-July (Turner *et al.*, 1992), but predators did not appear to regulate the population of zebras in the Serengeti (Bertram, 1984). Predation of the Przewalski horses was quite low, only a mean of 2.8 horses a year were taken (n = 14, 31% of all deaths between 1994 and 1999, 16% of all foals born in this time) all of which were one year old and less. Although its effect will have been greater when the population was smaller, it is unlikely that predation is affecting the current population growth (about 10% per year (Bouman, 2001)).

Vigilance in African antelopes changed seasonally, as they needed to spend more time feeding at certain times of year so were able to devote less time to vigilance (Underwood, 1982). In the spring the Przewalski horses spent more time feeding, yet were also able to be more vigilant at that time. As the horses need to feed more in the spring and autumn to gain weight, vigilance will be more costly and so must be necessary to the animals. A good deal of the vigilance of the Przewalski horses appeared to be directed at conspecifics and so may not be affected by predation, but rather that they are seeking cues to good food patches. However it is also possible that scanning was to detect signs of vigilance in other harem members (Lima, 1995). The breeding season is in the spring, so heightened vigilance in that season may also be related to stallions being wary of rivals. Males tended to be more vigilant than females during the rut of many species, but then both sexes had similar levels after parturition (Quenette, 1990). Animals are also likely to be picking up cues from each other to aid group cohesion (Underwood, 1982).

More evidence of vigilance being towards other horses rather than predators comes from the time of day when most vigilance occurred. If predation was affecting the animals then more vigilance would be expected at dawn and dusk, and at night, when predators are most active, as was seen among African ungulates (Schaller, 1976; Scheel, 1993). However least vigilance was observed at these times and during the middle of the day, and most when the horses were active during the day and so likely to be monitoring each other. Roberts (1988) found that vigilance in rabbits decreased as the evening proceeded and with higher temperatures, but could not find an explanation for this from the data.

It is impossible to determine exactly what an animal is looking at, but in this study an object or animal that the eyes and ears were pointing at was used to provide a rough guide. Despite this most of the animals' vigilance was due to an unknown stimulus. This could be due to the better senses of a horse, compared to a human, but is likely to be due to the horses general scanning of the landscape. Unfortunately it is impossible to know if this was for better food patches, other harems, or predators, although Berger (1978) found no difference between scans for conspecifics and those for predators in bighorn sheep.

Although data were not gathered on vigilance in different habitat types, the horses did appear more 'spooky' when in the woods or gullies, or stand resting with their heads leaning against rocks, tending to be more liable to bolt if disturbed. Other

studies have shown a habitat effect on vigilance with animals tending to be more vigilant when they were farther from habitat where they could evade predators (e.g. Dall's sheep (Frid, 1997)), or where chances of spotting predators was reduced (e.g. Townsend's ground squirrels (Sharpe & Van Horne, 1998)). The low frequency of vigilance overall could have been affected by the openness of the habitat in which the horses spent most of their time, as among other factors the risk of predation of African ungulates varied with the available cover (Scheel, 1993).

Certain factors affected the vigilance of the horses. Older, more aggressive horses that had spent longest in a harem and were higher ranking tended to be more vigilant at HNP. However, there are contradictory results on the influence of age and rank on vigilance in the literature (Quenette, 1990), for example there was no relationship between vigilance frequency and age in the Great Basin horses (Berger, 1986). There is also ambiguity on the influence of sex on vigilance in horses. The stallions were more vigilant than the mares in two of four harems in HNP. Berger (1977) found that stallions were less nervous than mares in the Grand Canyon, but in the Great Basin they were more vigilant (Berger, 1986). Zebra females tend to be predated more than males (Berger, 1983b), and if the same pattern is true for them, it is possibly their lower vigilance as well as their lesser strength that makes them more susceptible. There was also no difference in vigilance between mares with foals and those without, although Berger (1986) found that parous females were as vigilant as stallions in the spring in the Great Basin.

There was no evidence that the Przewalski horses at HNP were not vigilant enough and were unaware of predators, although vigilance occurred at a low frequency. One observation was that the Przewalski horses were more curious than afraid of a wolf (pers. obs.), but they have also been reported to form a defensive circle around foals and confront wolves aggressively (pers. comm. Mongolian rangers). Comparison with captive Przewalski horses would be useful to examine any difference in vigilance frequency. It would also be useful for further research to be carried out on the population at HNP to examine any changes in their vigilance, and if they begin to show a relationship between group size and vigilance as more harems become available to observe.

4.4 SUMMARY

- The mean frequency of aggressive acts among the horses at HNP was 0.35 acts horse^{-1} hour^{-1}. This is lower than any other observed population of horses. There was no difference among the harems or years, but there was a positive correlation between group size and frequency of aggression.
- Herd, bite threat and hind leg kick were the most frequent agonistic behaviours. Retaliatory or defensive behaviour (expressed mostly as hind leg kick) was observed in only 10% of all interactions. In all other cases the recipient of aggression moved.
- Stallions were more aggressive than mares, who were more aggressive than juveniles. Aggression by foals was very rare. The most frequent behavioural elements observed in stallions were herd and fight, and there was no difference in the frequency of aggression among them. Mares were observed to bite threat and hind leg kick most frequently, and there was no difference among the mares of the different harems.
- Most aggression was directed down the dominance hierarchy, but aggression was not directed to animals immediately above or below in rank.
- Not all harems in all years had a significantly linear dominance hierarchy. The stallion was most dominant in all harems in all years except for Bayan's in 1998 and 1999. This harem in these years was also the only one that had a triangular relationships among the mares.
- There was a negative correlation between rank position and aggression (acts hour^{-1}), age and tenure in the harem overall, but this tendency varied among harems and years. Mares that newly joined a harem were normally low in the hierarchy, even below the juveniles, but appeared to increase their rank in sunsequent years. The presence of a foal had no affect on a mare's rank.
- Associative behaviours appeared to have a primarily hygienic function, although social factors could not be ruled out. Sample sizes were small.
- Mutual grooming and stand resting together were the most frequent associative behaviours. Play and head rubbing were rare. Most interactions occurred between mares and juveniles.

- Most mutual grooming was on the withers and occurred in the spring and autumn, and morning and evening. There was no correlation between mutual grooming partner and relatedness (except in Margad's harem), tenure in the harem, age or aggression.
- Most stand resting together occurred in the summer months, and in the middle of the day. There was no correlation between stand resting together and relatedness, tenure in the harem, age or aggression.
- Most marking was observed in the breeding season when most unknown stimuli and mare eliminations, and relatively few stud piles were marked.
- Stud piles were sniffed before and after marking and dung was normally deposited. They tended to be found on paths and ridges and were located throughout the home ranges. It is likely that marking stud piles provided stallions with information on the movements of other harems, and so enabled them to avoid each other, as well as orienting them within their range.
- Mare eliminations were found on the grass and were sniffed before, but not after they had been marked with urine. Marking of mare eliminations is likely to show associations between mares and stallions, and so may reduce the potential for fights between stallions.
- Almost all marking was carried out by harem stallions. Differences between the behaviour when marking stud piles and mare eliminations means that they should be analysed separately in future studies.
- There was no correlation between group size and vigilance.
- Most vigilance was observed in the spring and autumn, which is when most foals were taken by wolves, but this also coincides with the breeding season.
- Less vigilance was observed in the early morning and evening, when predators would be expected to be most active. The main known stimuli causing vigilance were 'unknown' and the landscape, but harem members, the harem stallion and other harems also elicited vigilance.
- It is likely that most vigilance of the horses was to aid group cohesion, to examine the alert state of other horses or to scan for food patches.
- Stallions were more vigilant than mares, who were more vigilant than juveniles. There was a positive correlation between vigilance and aggression, age and tenure in the harem, and a negative correlation between vigilance and dominance rank.

Chapter Five

Effects of flies

Chapter 5. Effects of flies

5.1 INTRODUCTION

5.1.1 Biology of flies

Parasitism has evolved in almost half of the orders of insects (Askew, 1971). Although all species of lice (Mallophaga and Anopleura) and fleas (Siphonaptera) are ectoparasites of mammals or birds, the main hosts of most orders (e.g. Hymenoptera and Neuroptera) are insects (Askew, 1971). The Diptera are the only insects that infest the bodies of vertebrates, and will affect the lives of mammals by expanding wounds, extracting the cost of a blood meal or by passing on diseases (Askew, 1971). Of the 90 000 known species in this order, 11 000 parasitise vertebrates or invertebrates (Askew, 1971).

Diptera are typified by having one pair of wings on the second or middle segment of the thorax with the second pair of wings modified to halteres, which act as gyroscopic stabilisers in flight (Oldroyd, 1964). The order is very diverse, with a large range in size (from more than seven centimetres to less than five millimetres in length) and a wider range of form of mouthparts than any other order, yet the same evolutionary adaptations appear independently in several families (Oldroyd, 1964). In particular the development of some kind of mechanism to penetrate the skin to suck blood has evolved in all three suborders; for instance, in the Nematocera, the Culicidae (mosquitoes) pierce the skin and seek a capillary; in the Brachycera, the Tabanidae (horse flies) pierce the skin and consume blood from the surface; and in the Cyclorrapha, the Glossinidae (Tsetse flies) abrade the skin to draw blood (Askew, 1971). The form of the mouthparts is diverse among the families depending on the mode in which the food is obtained, but in most the labium is the chief part of the proboscis (Davies, 1988).

Although many families parasitise plants or insects, or have other lifestyles, only parasites of mammals will be discussed here (Table 5.1). The form of attack can be divided in to two forms – blood feeding, and myiasis (infestation with larvae), which can be either accidental, or necessary for the development of the larvae. In all forms of attack there is the possibility of disease or infection being passed on, and in this way the effect of a bite may exceed the initial loss of blood.

Table 5.1. Families of Diptera in which one or more species parasitise mammals.

Common name	Family	Feeding strategy		
		Blood feeding	Myiasis	
			Facultative	Obligatory
Suborder Nematocera				
Window flies	Anisopodidae		Yes	
Mosquitoes	Culicidae	Yes		
Biting midges	Ceratopogonidae	Yes		
Black flies	Simuliidae	Yes		
Sand flies	Psychodidae	Yes	Yes	
Suborder Brachycera				
Horse flies, clegs	Tabanidae	Yes		
Snipe flies	Rhagionidae	Yes		
Suborder Cyclorrapha				
Coffin flies	Phoridae		Yes	
Hover flies	Syrphidae		Yes	
	Piophilidae		Yes	
	Ephydidrae		Yes	
Blow flies	Calliphoridae		Yes	Yes
	Neottiophilidae			Yes
	Chloropidae			Yes
Bot flies	Gasterophilidae			Yes
Bot/warble flies	Oestridae			Yes
House flies	Muscidae	Yes	Yes	Yes
Tsetse flies	Glossinidae	Yes		
Louse flies	Hippoboscidae	Yes		
Bat flies	Nycertibiidae	Yes		
Bat flies	Streblidae	Yes		

After (Askew, 1971).

Blood sucking is confined to the females of the Nematocera and Brachycera, but both sexes of some species of Cyclorrapha are parasitic (Davies, 1988). The most generalised form of feeding is pool feeding, in which a puncture is made in the skin and the blood is consumed from the surface (e.g. Tabanidae, Calliphoridae and Muscidae). Some families (e.g. the Culicidae) have become more specialised and pierce the skin until they encounter a capillary, from which they draw blood (Davies, 1988). In the Nematocera and Brachycera the mandibles and maxillae have been developed into piercing stylets with a labium to mop up the blood and to sheath the mouthparts (Oldroyd, 1954). Many of these species also inject a form of anti-coagulant in their saliva (Davies, 1988). Several families of the Cyclorrapha feed by folding back the labia to expose the prestomal teeth with which they scratch the skin surface to draw blood (Oldroyd, 1954). In non-predatory species the labium and labella are also used to draw up liquid food like a sponge.

Biting flies find their hosts by a variety of methods and host location will be affected by climatic conditions and endogenous rhythms (Evans, 1984). Insects that fly primarily during the day are attracted to moving objects. Tabanidae have been seen following cars (Evans, 1984), and a response was elicited from Glossinidae when a black screen four feet long and three feet high was moved fifty yards away from them (Askew, 1971). Convection currents from a warm body, which produce a temperature gradient and will carry odours, have been shown to attract Culicidae, Simuliidae and Glossinidae (Evans, 1984). Tabanidae are attracted to carbon dioxide, and this will also activate Culicidae, acting as a releaser for feeding behaviour in this family (Evans, 1984). In addition certain colours are said to attract flies (Lewis & Taylor, 1967). Fewer Tabanids on dark coloured young than on white adult Camargue horses has been attributed in part to the different attraction of the colours (Duncan & Vigne, 1979). Biting flies are abundant through the summer months (Oldroyd, 1964), and tend to be more active when the wind speed is moderate, as in mild winds the flies may not be able to find their hosts, and in strong winds the energetic costs of flying are too high (Rubenstein & Hohmann, 1989).

Dipteran larvae are found in almost every medium from aquatic (e.g. Simuliidae) to dry sand (e.g. Psychodidae), but many families need water or damp conditions in which to lay their eggs and for the larvae to develop (Oldroyd, 1964). Flies from the Calliphoridae lay their eggs on carrion, but will also infest wounds. They have been said to be beneficial to wounds as they may excrete substances that kill bacteria and others substances that stimulate phagocytosis, but some species will also consume living tissue (Evans, 1984). Obligate myiasis is also seen in the Calliphoridae. Most notorious is the screw-worm (*Callitroga*, *Chysomya*, and *Wohlfahrtia* spp.) which can turn a minor injury into a major wound as they infest it, and can eat the flesh to the bone (West, 1992). Other species form a boils in which the larvae develop (e.g. species of the genera *Cordylobia*) (Askew, 1971). As well as infestation of wounds, facultative myiasis occurs when larvae are eaten, and survive in the stomach. This has been reported for the Phoridae and some species of Calliphoridae (Oldroyd, 1964).

Obligate myiasis families include those whose larvae are intestinal parasites, as well as external. These include the Oestridae, which live as larvae in the nasal cavities of grazing mammals, or in the subcutaneous tissue (West, 1992). Of most relevance to this thesis are the Gasterophilidae, in particular species belonging to the genus *Gasterophilus* which are exclusively parasites of equids. The life histories of the

different species of *Gasterophilus* differ. *G. pecorum* lays eggs on grass, which then hatch after they have been eaten, whereas *G. haemorrhoidalis*, *G. intestinalis* and *G. nigricornis* lay their eggs on the hair of the host (Askew, 1971). These latter three species differ on the part of the body that the eggs are laid (lips, legs or back, and cheeks respectively), the stimulus required causing them to hatch (moisture, licking or spontaneously), and the part of the alimentary canal where they attach (from the soft palate to the duodenum) (Askew, 1971). However in each species the larvae burrow through the epidermis of the lips or tongue before passing to the stomach. It is interesting that bot flies and warble flies have been observed to cause great distress in cows and horses, to the extent that livestock have been lost and production reduced through the "mad chasing of cattle" (West, 1992), yet the flies do not directly cause pain and it is the larvae that form the cost to the host.

5.1.2 Effect of flies on their host

All flies are likely to form a cost to an animal either directly by taking blood, nutrients or exacerbating a wound, or indirectly through disease or causing feeding to cease. The most extreme example of the effect of flies was when Golubatz flies (*Simulium columbaschense*) caused the death of 20 000 horses, cattle, sheep and goats in Rumania, Bulgaria and Yugoslavia in 1923, after they swarmed from the Danube (Oldroyd, 1964). In this case it appears that most of the deaths were not caused by blood loss, but through anaphylactic shock and toxaemia (Askew, 1971). Although attacks of this magnitude are rare, even at low numbers flies can have strong effects on the behaviour of animals.

Except in extreme situations, endoparasites have a more direct effect on the condition of horses than ectoparasites (Rubenstein & Hohmann, 1989). A large number of larvae can accumulate in the gut of horses and although the larvae rarely directly cause death, they can block passageways and cause discomfort to their hosts (Oldroyd, 1964). However, without an autopsy or experimentation it is hard to tell whether the loss of condition of infested horses is caused by Diptera larvae or other internal parasites. Rubenstein and Hohmann (1989) came to the conclusion that as the negative effects of endoparasites override those of ectoparasites, internal parasites will affect the social structure of horses and have more of an impact on their body condition, but flies will have a stronger effect on their behaviour. Fewer flies were on each horse when they were in large groups, but each individual had more endoparasites than horses in

smaller groups, as large groups generate more dung around which they would feed, and so consume eggs. Therefore there must be an upper limit to group size where the costs of the endoparasites exceed any benefits of fly relief.

The effect of flies on horses has been well studied in the Camargue population and similar results have been observed in other feral horse populations. Both the abundance of biting flies and the weather were the best predictors of the habitat use of Camargue horses for non-feeding activities in the summer (Duncan, 1983). The abundance of flies increased with the temperature in the morning, became stable at the hottest time of day and then decreased in the late afternoon (Hughes *et al.*, 1981). As the flies became more active and abundant the horses would move to patches of bare or sparsely vegetated ground (Hughes *et al.*, 1981), away from their preferred feeding areas (Duncan, 1983). Duncan and Cowtan (1980) observed a third fewer tabanids on the horses when on bare ground than in the more vegetated areas. However Hughes *et al.* (1981) found no difference in the fly load on bare ground, but that the wind speed was greater than in vegetated areas; this would negatively affect the fly activity.

Other studies also report use of bare patches of ground, such as beaches or bays (Keiper & Berger, 1982; Rubenstein & Hohmann, 1989; Rutberg, 1987; Zervanos & Keiper, 1979), snow patches (Keiper & Berger, 1982), or use of ridges (Keiper & Berger, 1982) as refugia from flies by horses, or caribou (Bergerud, 1974) and red deer (Clutton-Brock *et al.*, 1982). All of these places are bare of vegetation and exposed to the wind. As the horses cannot eat at these places, (they are normally observed stand resting), or else would forage less profitably, use of them reflects a choice between feeding and avoidance of insects.

Penzhorn (1984) and Joubert (1972) reported that zebras stand in the shade when they rest. Camargue horses stayed in the open where there were fewer flies, even though they could have reduced their temperature in the shade (Duncan & Cowtan, 1980). However it is possible that in Africa, loss of heat becomes more important than avoiding flies. Caribou disperse from their calving grounds as flies become more abundant and they were observed to rest in the shade in forest to avoid flies which were less abundant there (Bergerud, 1974). It is unlikely that the shade was used to cool down, because the temperature was only 1.5°C cooler than in the open (Bergerud, 1974).

Animals can use similar mechanisms to protect themselves from parasites and to avoid predators, such as the encounter-dilution and selfish herd effects (Mooring &

Hart, 1992). This has been shown in several studies where larger groups of horses had fewer flies per individual than smaller groups (Duncan & Vigne, 1979; Rubenstein & Hohmann, 1989; Rutberg, 1987). In the Camargue and in Japan larger groups formed in the summer than during the rest of the year (Duncan & Vigne, 1979), but this has not necessarily been observed in other populations (Rutberg, 1987). However in all populations there is a tendency for horses to stand close together when flies are abundant.

Deaths of horses caused by attacks of flies have been reported in Mongolia (Allen, 1998). The local nomads are normally aware of the occurrence of biting flies and move their livestock away from areas of high numbers, but swarms are ephemeral and can be unpredictable. When exploring an area for future potential release sites the abundance of biting flies should be a major issue. Their abundance will affect the length of time the horses spend feeding during the summer months, and, together with other parasites, have implications for the health of the population as vectors of disease. However, no study of the feasibility of sites for reintroductions has examined this (FAO, 1986; Zimmermann, 1998). It is important to know how Przewalski horses cope with flies, and to have an idea of the habitat they select for insect relief so that it can be considered in future reintroduction sites or management plans.

5.2 RESULTS

5.2.1 Species abundance

As a pilot study in 1998, 50 fly traps (7 water traps and 43 sticky traps) were set over eight days in July and August. In total 114 insects were caught, 94 of which were dipteran flies (82%). Between 0 and 15 insects were caught in each trap. The flies were of seventeen different 'types' (Appendix XI), but they were not collected and it was not possible to identify them further. There was little difference in the abundance of flies between July and August (56 and 51 flies respectively). Most flies were caught in Khaan's home range. Fifty-three flies were caught there in 9 traps set, whereas in Paritet's home range only 27 flies were caught in 20 traps, and in Bayan's 27 flies in 27 traps.

In 1999 the trapping regime was changed (see Methods, Section 2.3.3.1) and more flies were caught. 1045 insects (696 dipteran flies (67%), 349 other insects) were caught in 47 traps set in various places in the horses' home ranges, focussing on grazing and resting areas, on 9 days between May and September. More flies were caught in May and June than in July and August (Kruskal-Wallis $H = 13.67$, $df = 3$, $p = 0.003$), however there was no difference in the total number of insects caught each month ($H = 7.71$, $df = 3$, $p = 0.052$). September was excluded from the analysis because only one trap was set in this month.

Insects were placed in sample jars of alcohol, taken back to QMUL and identified to family level. Eighteen families of flies and five families of other insects were found (Table 5.2). Although the flies were not identified to species level, several were 'typed' and are likely to equate to species. In addition, there were 150 insects (13 types) which were not removed from the traps, only a description was made. These were assigned to a family based on the description. Thus for each family there is a known total of the number of flies caught (from those collected from the traps), and the possible maximum number that includes those not removed (Table 5.2). Muscidae, Asilidae and Phoridae were the most abundant families; Bombyliidae, Gasterophilidae, Lonchopteridae, Sepsidae, and Tabanidae were rare (Table 5.2).

Table 5.2. Flies caught in traps in HNP, 1999. Known number indicates the number of flies of that family of which at least one type specimen was identified in the laboratory. Possible number of flies are those with a similar description to the type specimen but not removed to the lab. The number of different 'types' of each family is shown.

Common name	Family	Number of types	Known number	Possible number	% of possible number found at different trapping areas					
					Grazing places		Resting places		Woods	
					Stream	Valley	Rocks	Ridge	In woods	Outside woods
House flies	Muscidae	11	73	97	32	24	24	5	7	8
Robber flies	Asilidae	1	53		17	83	0	0	0	0
Coffin flies	Phoridae	4	52	82	39	35	13	4	4	4
Crane flies	Tipulidae	1	30		100	0	0	0	0	0
	Dolichopodidae	8	29	39	43	50	7	0	0	0
Gall midges	Cecidomyidae	1	16	19	29	57	0	0	14	0
Blow flies	Calliphoridae	5	14	2	31	23	31	0	8	8
Snipe flies	Rhagionidae	1	11	9	22	11	33	11	0	22
Dragonflies	Odonata	2	9	12	33	17	50	0	0	0
Chironomids	Chironomidae	1	5		33	33	33	0	0	0
Lacewings	Neuroptera	1	4	3	0	67	0	0	0	33
Mosquitoes	Culicidae	1	2		100	0	0	0	0	0
Fungus gnats	Mycetophylidae	1	2	3	50	0	50	0	0	0
Bee flies	Bombyliidae	1	1		0	100	0	0	0	0
Bot flies	Gasterophilidae	1	1		0	100	0	0	0	0
	Lonchopteridae	1	1		100	0	0	0	0	0
	Sepsidae	1	1		0	100	0	0	0	0
Horse flies	Tabanidae	1	1		0	0	0	0	0	0
Wasps	Hymenoptera	5	5	1	60	40	0	0	0	0
Booklice	Psocoptera	1	4		100	0	0	0	0	0
Beetles	Coleoptera	1	3		100	0	0	0	0	0
Springtails	Collembola	2	2		0	100	0	0	0	0
Bugs	Hemiptera	1	1		100	0	0	0	0	0

5.2.2 Spatial distribution

5.2.2.1 Trap data

Although most insects were found by the stream, there were fewer than expected found in the valley, inside and outside the woods and at the rocks ($X^2 = 108.98$, df = 5, p = <0.0001). In addition, a greater number of families was represented in the catch by the stream and valley than expected ($X^2 = 36.41$, df = 5, p = <0.0001; Table 5.2). The type diversity differed across the trap areas (Table 5.3). The stream and valley had the greatest type diversity, but were least even. This reflects the large numbers of families of flies that were caught in these areas.

Table 5.3. Diversity and evenness of types of fly at different trap areas. S = number of 'types' at each site. H' = the Shannon-Wiener diversity index, 0 - H'_{MAX} (H'_{MAX} = logS). J' = Evenness measure based on the Shannon-Wiener function (range 0 – 1).

	Stream	Valley	Ridge	Rocks	Inside woods	Outside woods
S	29	28	4	16	5	7
H'	1.08	1.15	0.58	0.96	0.66	0.74
H'_{MAX}	1.46	1.45	0.60	1.20	0.70	0.84
J'	0.74	0.79	0.97	0.80	0.94	0.88

5.2.2.2 Count data

There was an association between the abundance of flies across the different sampling sites between the trap data and count data derived from counting flies on a horse ($X^2 = 367.24$, df = 5, p = <0.0001). In particular more flies than expected were found in traps at the stream, valley and at the rocks than were counted on a horse, and more flies than expected were counted on a horse inside and outside the woods than were caught in traps (Table 5.4). The count sampling provided a larger data set than the traps, with 6421 flies counted on 427 horses between June 1998 and November 1999, whereas only a total of 1045 insects was caught in traps.

Table 5.4. Per cent of flies found at different sampling areas per horse and per trap.

Sampling area	Count data	Trap data
Stream	23	30
Valley	11	27
Ridge	16	11
Resting rocks	9	26
In woods	23	3
Outside woods	19	4

The aim of the count data was to reveal if there was any difference in abundance of flies between the two main areas used by the horses – grazing places (the lower valley and stream) and resting places (ridges and by rocks). The horses also rested in woodland near the ridges, and counts were made to compare fly numbers in the woods and the area immediately outside them. However the sample sizes for these areas were smaller than for the grazing and resting areas (Table 5.5).

There was a significant difference between the number of flies counted on horses in these four main areas ($H = 10.04$, $df = 3$, $p = 0.018$). There was no difference in the number of flies on a horse between the grazing and resting areas, nor between inside and outside the woods. However more flies were counted on a horse both inside and outside the woods than at the resting areas, although there was no difference between the woods and grazing areas (Table 5.5).

Table 5.5. The median value of number of flies horse^{-1}, temperature (°C) and wind speed (km hr^{-1}) at different areas used by the horses. IQR are shown in brackets. Wind speed values are for 1999 only, so separate sample sizes are given.

Area	n	No. flies	Temperature	n	Wind speed
Grazing	173	8 (0.5-23.5)	19 (15-24)	111	2 (0-7)
Resting	153	6 (0-17.5)	18 (12-25)	102	4 (0-8)
In woods	50	15 (1-34.3)	18 (15-23.3)	31	0 (0-0)
Outside woods	51	15 (2-23)	17 (16-24)	30	4.5 (0-11.75)

Both temperature and wind speed could affect relative fly abundance and horse temperature regulation. There was no difference in temperature between the areas ($H = 0.15$, $df = 3$, $p = 0.985$), but the wind speed was greater outside the woods and at the resting places than inside the woods and at the grazing places ($H = 31.25$, $df = 3$, $p = <0.0001$) (Table 5.5).

There was a difference between the number of flies found on the different colours of horse, with palomino horses being the only colour to have fewer flies than expected ($X^2 = 14455.58$, $df = 5$, $p = <0.0001$; Table 5.6). More flies were found on the haunch of horses than on the head or neck and shoulder ($X^2 = 1022.96$, $df = 2$, $p = <0.0001$; Table 5.7).

Table 5.6. Mean number of flies on horses of different colours (± standard deviation).

Colour of horse	n	Number of flies per horse
Bay	47	27 ±28
Chestnut	6	23 ± 13
White	180	18 ± 20
Dun	115	12 ± 13
Black	76	6 ± 9
Palomino	6	3 ± 3

Table 5.7. Per cent of flies on different parts of the horses body (n = 428 horses).

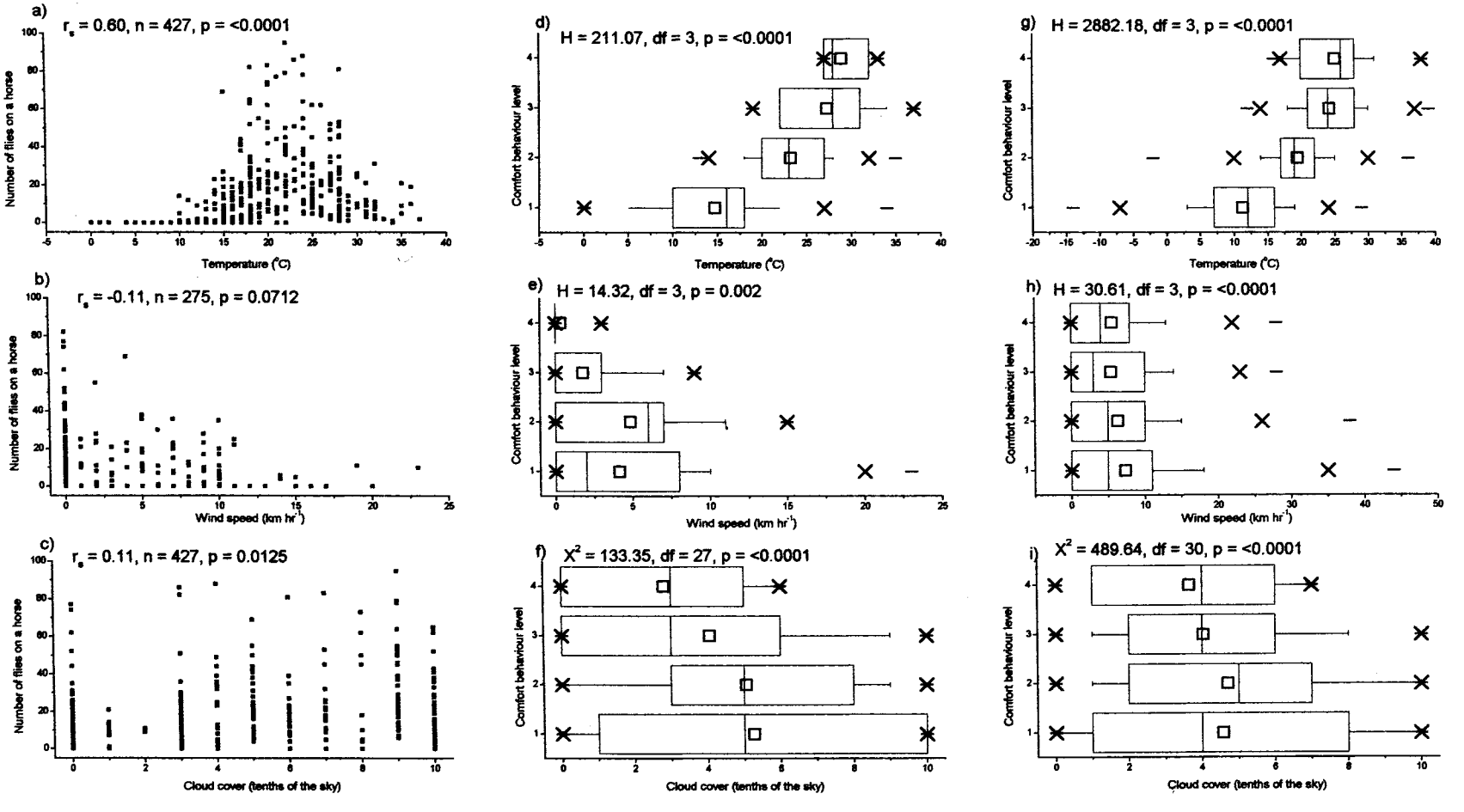
Part of body	Per cent of flies
Head	17
Neck and shoulder	34
Haunch	49

5.2.3 The influence of environmental conditions on fly abundance

The effects of environmental conditions were only tested on the count data, not the trap data. Fewer flies were counted on horses in April, October and November than in the other months (there was no difference between these months) ($H = 179.31$, $df = 7$, $p = <0.0001$). There was a positive correlation between the number of flies and temperature, but flies were most abundant when the temperature was between 15°C and 30°C (Figure 5.1a). No comfort behaviour (comfort behaviour level 0) was observed when the temperature was low, and the comfort behaviour level increased with the temperature (Figure 5.1d). There was no significant correlation between the number of flies and wind speed (Figure 5.1b), but the comfort behaviour tended to be less when the wind was stronger (Figure 5.1e). There was a significant but only a very small positive correlation between the number of flies on a horse and the cloud cover (Figure 5.1c). Cloud cover also had an effect on the comfort behaviour of the horses (Figure 5.1f), although two tenths cloud cover had to be removed from the analysis due to a small sample size. There was little correlation between the environmental variables (Appendix XII).

The data were further explored by carrying out a stepwise multiple regression with count of flies as a dependent variable and month, hour, temperature, wind speed and cloud cover as independent variables. The maximum adjusted r^2 value with all

Figure 5.1. Graphs to show the similar effects of fly abundance on the comfort behaviour of ridden horses and Przewalski horses. Graphs a - c show the number of flies on a horse at different environmental variables. Graphs d - f show the comfort behaviour of the ridden horses at the same conditions as in graphs a - c. Graphs g - i show the comfort behaviour of the Przewalski horses at different environmental conditions.



variables included was 17.5%, with just temperature 12%. This indicates that none of the environmental variables satisfactorily explains the number of flies on a horse.

More flies were counted on the horses when they were stand resting (mean = 24 flies horse^{-1}, sd = 21) than when they were grazing or standing (mean = 16 flies horse^{-1}, sd = 18 or mean = 11 flies horse^{-1}, sd = 17 respectively) (X^2 = 12080.39, df = 2, p = <0.05). It is likely that the horses would stand rest when flies were abundant because they could not or would not graze. Instead they exhibited a higher level of comfort behaviour. However, the horses' tendency to stand rest at higher fly levels may reflect other factors. For example, when it is hot, and flies are more abundant generally, the horses will sweat more, and may attract more flies. There were fewest flies on a horse at low levels of comfort behaviour (X^2 = 16452.84, df = 3, p = <0.0001; Table 5.8).

Table 5.8. Mean number of flies on a horse at different levels of comfort behaviour (± standard deviation).

Comfort behaviour level	n	Number of flies
0	264	9 ± 14
1	102	26 ± 19
2	50	24 ± 23
3	11	17 ± 26

5.2.4 The effect of flies on Przewalski horses

The responses of the Przewalski horses to flies, expressed as comfort behaviour (see Methods, Section 2.3.1.1 for details), appear to show similar results to the more quantitative study of the fly count on a ridden horse (Figure 5.1). Results of the comfort behaviour of all harems in all years pooled were used for the analysis. Generally, there was an increase in the level of comfort behaviour with temperature (Figure 5.1g). There was a positive correlation between the temperature and the elevation where the horses were observed (r_s = 0.51, n = 5252, p = <0.0001), and a positive correlation between comfort behaviour and elevation (r_s = 0.50, n = 5252, p = <0.0001). The horses tended to have a lower level of comfort behaviour when the wind speed was higher (Figure 5.1h), and there was an association between comfort behaviour and cloud cover (Figure 5.1i). When there was some cloud (1/10 – 7/10 cloud cover) there were fewer observations of no comfort behaviour than expected,

but comfort behaviour levels 1 to 3 were all represented more than expected. However, when the sky was either completely clear, or greater than 8/10 cover, there were more observations of no comfort behaviour than expected, but fewer observations of comfort behaviour levels 1 to 3 than expected. The comfort behaviour of the Przewalski horses was highest from June to August ($H = 1687.47$, $df = 7$, $p = <0.0001$), and in the middle of the day ($H = 219.44$, $df = 18$, $p = <0.0001$), which is when flies were most abundant.

There was an association between comfort behaviour and concurrent maintenance behaviours of the horses (Table 5.9; $X^2 = 521.70$, $df = 9$, $p = <0.0001$). Lying down was excluded from the analysis as no comfort behaviour (comfort behaviour level 0) was observed during this activity, however it is likely they only lay down when there were few flies. The horses grazed more than expected when no comfort behaviour was shown, but at all other levels less grazing than expected was observed. More moving than expected was seen at all comfort behaviour levels except 0. There was less stand resting than expected at both no comfort behaviour, and at level 3.

Table 5.9. Activity of the harems at different levels of comfort behaviour (%).

	Comfort behaviour level			
Activity	0	1	2	3
Grazing	65	50	32	12
Lying down	4	0	0	0
Moving	12	14	15	39
Standing	4	5	8	25
Stand resting	16	32	44	24

As has been discussed in Chapter 3 the horses had definite daily movements up and down the mountains. Although there is no direct evidence that this was caused by the flies, the migration to a higher elevation occurred during the middle of the day, particularly in the warmer months, when flies were most abundant.

5.3 DISCUSSION

Flies were found to be most abundant during the summer months by both the fly traps and the flies counted on a ridden horse, and it was in these months that the Przewalski horses exhibited the most fly avoidance behaviour. As in other studies, most flies were observed when the temperature was between 20° and 30°C (Rubenstein & Hohmann, 1989), and this was reflected in the comfort behaviour of the Przewalski horses. Although there was no difference in the number of flies counted on a ridden horse at different wind speeds, wind had an effect on the comfort behaviour of the horses, suggesting that wind affected either the flies around the horses, or their effects.

At low levels of fly abundance the Przewalski horses were able to graze, and had low levels of comfort behaviour, but when fly abundance and temperature increased, the horses spent more time stand resting. When these factors increased further the horses were forced to move to seek refuge. However, more flies were counted on ridden horses when they were stand resting than when grazing. It is possible that this is because ridden horses were unable to seek refuge from the flies, but it could also be due to disturbed animals spending less time eating. Przewalski horses also would stand rest when fly abundance was high, and this behaviour has been observed in the middle of the day during summer in all horse populations (Wells & von Goldschmidt-Rothschild, 1979; Zervanos & Keiper, 1979). Groups of horses standing together, swishing their tails over each other is a common sight (Tyler, 1972). This movement will both prevent flies from settling and brush them off, and standing in a group may make the horses less apparent to flies, as well as reducing the likelihood of each individual being attacked (the encounter-dilution effect; Mooring and Hart (1992)).

During the middle of the day, and particularly during the summer months, the horses were observed to move up the slopes from their grazing places to rest by rocks near ridges or in the forest. This movement was associated with an increase in temperature, so was presumed to be caused by an increase in abundance of flies. However there was no difference in the number of flies between the grazing and resting places, and the comfort behaviour of the horses was higher when they were at higher elevations. As the wind speed was greater at high places, which the Przewalski horses used when the temperature increased, it is likely that the horses used high, bare, rocky areas because the fly activity would be lower, as was found in the Camargue (Hughes *et al.*,

1981). The higher comfort behaviour could also be a reaction to the heat. More flies occurred by the stream, which ran through the grazing areas, than in any other area, thus it is most likely that the horses moved to the ridges to escape insects, but are followed by the flies. This would result in the difference in spatial abundance of flies found by the trap and count data. By exhibiting a high level of comfort behaviour and standing in groups in places of higher wind the horses were able to minimise the effects of the flies better than when grazing separately.

The woods were used by the horses for resting during the summer even though there was no difference in temperature from the resting places and there were more flies. Therefore the horses use of the forest must have been to provide shade. Although the temperature was lower at the rocks it was rarely possible for the horses to get out of direct sunlight. Reindeer also used forest for shade (Bergerud, 1974), and zebras were observed to rest in the shade during the heat of the day (Joubert, 1972; Penzhorn, 1984). Camargue horses were observed to stand on bare ground in the sun, even though they may have been cooler in the shade (Hughes *et al.*, 1981), but it is probable that shade is more important at the altitude of HNP.

The Camargue horse and some Iberian breeds of horse are born nearly black, and become whiter as they mature. This has been thought to be an adaptation to avoid flies, and fewer flies were observed on Camargue foals (Duncan & Vigne, 1979). This appears to be reflected in this study because fewer flies were observed on black horses than white. Fewer biting flies were also observed on foals of other populations and may be related to their lower metabolic rate, and consequently a lower emanation of carbon dioxide which will attract tabanids (Rutberg, 1987). Size, therefore, may also be a factor.

This study did not examine the different species of flies, which would provide information on the direct effects of the flies on the horses, but knowledge of the families can provide an idea of the likely effects. Several of the families caught in the traps contain species that parasitise other insects, but will have no effect on the horses (e.g. the Asilidae and Bombyliidae). Phoridae are not obligate parasites at either the larval or adult stage of development, but can survive within the gut if swallowed. Of most interest is the fact that only one Tabanidae was caught. This is unlikely to have been purely a result of the trapping method as very few tabanids were observed in HNP, whereas at the Tuul river fifteen kilometres away (just outside the park) tabanids and mosquitoes were abundant (pers. obs.). It is members of this family that

have been observed to have the great effects on horse behaviour that were described above, so it is interesting that they were rare at HNP, even though the horses were showing great aversion to flies. The reason for their absence could have been due to lack of habitat to lay their eggs as they need damp soil (Tashiro & Schwardt, 1953), which is rare in this arid region even by the stream. The presence of a ridge of mountains between the river and most of HNP could have prevented their colonisation of the area.

Only one fly from the Gasterophilidae was caught. Unlike the Tabanidae this is likely to reflect a bias in the traps because the larvae were present in the carcass of every dead Przewalski horse found and the eggs were observed on the fur of domestic horses in the area, suggesting that they were common. These flies have been observed to cause great distress to cattle and horses (West, 1992) and could be responsible for the horses' movements.

The other families of flies that could affect the horses are the Muscidae and Calliphoridae. Members of these families affect horses both by myiasis of wounds and spreading of disease, and also simply by flying around the heads of the horses and causing annoyance (West, 1992). Flies from these families together were the most numerous caught in the traps and are likely to be most responsible for the fly avoidance behaviour of the horses. Although the biting 'stable fly' *Stomoxys* sp. could be present, the reaction of the horses to cease feeding and rest when the other, non-biting, members of these families were abundant seems extreme when they cause little bodily harm to a healthy horse. All other studies of the effects of flies have assumed that the avoidance behaviour of the horses is caused by tabanids, and do not state the abundance of other species of fly. It has been thought that horses attempt to evade biting flies to avoid the pain of a bite, but perhaps annoyance is a larger factor in their movements than previously considered. However it is possible that the reintroduced horses had learned a strongly aversive response to flies when they were kept on pasture where tabanids were present. When affected by flies in Mongolia they may have the same reaction as to tabanids in Europe and the offspring will then learn this behaviour.

The effect of the Muscidae and Calliphoridae on wounds of the horses was also apparent. Several foals that were attacked by wolves, but not killed, subsequently died after their wounds became infested with maggots. Although other injuries caused by wolves could not be ruled out as a cause of death, the suffering undergone by the foals

was beyond doubt. At least three cases of vaginal infections were observed following the birth of a foal (one of these cases involved the manual removal of a dead foal from the mare). Flies feeding on excretions from the vulva of the mares probably passed on these infections. In all of the cases the mares lost condition and one mare subsequently died. Wolves killed both of the surviving foals, possibly as they were in poorer condition due to reduced milk yield of the mare. In one case the foal was observed attempting to drink more than actually nursing, although no quantitative data were obtained.

Therefore although there were few biting flies in HNP, the flies had a strong effect on the horses by causing them to stop feeding and move up to ridges to rest through the heat of the day in the summer, and also by passing on infection and disease and by myiasis. Future reintroduction sites should survey the local people for information on the occurrence and severity of biting flies. A site that may be potentially good for release due to few livestock may be empty because livestock cannot live there. One of the criteria for site selection should be the availability of places where horses can shelter from flies in the wind as this will affect its suitability. This may be particularly important in the acclimatisation phase after release.

5.4 SUMMARY

- 1045 insects (18 families of flies and five families of other insects) were caught in water traps during 1999. Muscidae, Asilidae and Phoridae were the most abundant families.
- Most insects, and a greater abundance of families, were found by the stream and in the valley than at the resting places of the horses.
- Flies counted on a horse produced a different picture of the spatial abundance of flies than the fly traps, since relatively more flies were counted inside and outside woods, and fewer at rocks and in the valley than were caught in traps.
- There was no difference in the number of flies on a horse between the grazing and resting areas, but more flies were found both inside and outside the wood than at the resting areas.
- There was no difference in temperature among these areas, but the wind speed was greater outside the woods and at the resting places than inside the woods and at the grazing places.
- Most flies were found in the summer using both the count and trap data; the count data also revealed more flies during the middle of the day. The Przewalski horses exhibited highest levels of comfort behaviour during these times.
- Exploration of the data with a stepwise multiple regression showed that environmental variables accounted for only 17.5% of the abundance of flies.
- The comfort behaviour of the Przewalski horses followed similar trends to that of domestic horses on which the number of flies were known.
- There was an increase in the level of comfort behaviour with increased temperature and there was a positive correlation between temperature and the elevation where the Przewalski horses were found.
- The horses tended to have a lower level of comfort behaviour when the wind speed was higher and the sky was either clear or covered with cloud.
- The Przewalski horses grazed when no comfort behaviour was shown, but then would stand rest as flies became more abundant, until a certain threshold when they would be forced to move to seek refuge.

Chapter Six

Conclusions

Chapter 6. Conclusions

6.1 Key findings

The overall aim of this project was to examine the behavioural ecology of Przewalski horses released into the wild at Hustai National Park, Mongolia, including studies on the horses' home range and habitat use and social behaviour. The literature concerning the points made below has been covered in the appropriate chapters.

It appears that the home range and habitat use of the Przewalski horses was very similar to that reported for feral domestic horses under comparable conditions. Although there was no trend in the change of range size with group size or time since release, there was a tendency for harems to establish a home range near their acclimatisation enclosure immediately after release, then in subsequent years to move further away, although they usually remained in the same valley. It is possible that there will be a greater relationship between range size and group size as the population grows and competition for space and resources increases.

There was some spatial overlap between adjacent home ranges, thus no evidence for exclusive range use. However, this might change as the population size increases and there is a need to monitor for signs of overgrazing in the most used areas. Both the degree of overlap among harems, and the subsequent impact on the vegetation is important with respect to the number of harems that can be supported by HNP.

The time budget and temporal habitat use of the horses was similar to other equid populations. For example, equids graze during the morning and early evening and rest during the middle of the day. Seasonal effects, such as spending more time grazing and less time resting in the colder seasons, have also been observed in feral populations, as well as use of ridges and bare ground to rest during the heat of the day during summer. Larger harems that had been free ranging for longer, spent more time grazing and less time resting than smaller, more recently released harems. This could be related to the vigilance of these harems, as would be predicted by the many eyes hypothesis, but could also be due to a need to become familiar with the habitat and deal with the stress of reintroduction.

The horses used vegetation in a similar way to that found in studies of feral horses; for example the most nutritious vegetation was selected in each season. It would

appear, therefore, that Przewalski horses have not lost those skills needed for survival in the wild while they were in captivity.

Currently there are few data on the behaviour of the Przewalski horses at HNP during the coldest months of the year. Further research into the home ranges, habitat use and mortality of the horses during the winter will be important.

Studying the bite rate of the horses did not prove to be very informative. This could be a fault of the methods used, for instance the bite rate of horses eating different plant species, rather than vegetation classes, might have provided more information on preferences. However, the decrease in bite rate through the year could reflect both the increasing availability of vegetation and the improved condition of the horses as they increase in weight throughout the summer. Pregnant or lactating mares had a higher bite rate than mares without a foal, even though there was no difference in the amount of time spent feeding, suggesting that there is an association between bite rate and condition.

The social organisation of horses at HNP was female (harem) defence polygyny similar to that observed in feral horses and plains and mountain zebras. No multi-male groups were formed during the study. Dominance hierarchies were evident, with older, more aggressive horses being more dominant. The stallion was most dominant in all harems except one (Bayan's), and had the highest frequency of aggression. The apparent lack of dominance by the stallion Bayan probably results from the rarity of aggression in this harem.

The observed frequency of aggression among the Przewalski horses at HNP was less than reported in any other study of horses. This is probably related to the lack of confinement and the natural formation of the groups. Dominance translates into reproductive success, but there were no obvious proximate benefits to being dominant, since the only resources that were contested for were shady places for resting in the summer. This could partly explain the low frequency of aggression. As the population increases the frequency of aggression will probably also increase, due to a higher number of interactions between horses and increased competition among them. It is therefore possible that forming dominance ranks is an intrinsic part of the behavioural repertoire of horses and its function may only become evident when conditions deteriorate and there is greater competition for resources.

Associative behaviour among the horses was rare, and appeared to have a primarily hygienic function. In the literature there is surprisingly little information on any

seasonality of horse associative behaviours. This could reflect the short time scale of some studies, but also most research appeared to be looking for the social significance of associative behaviour, rather than an overall function. There was no evidence for any relationship between social factors and associative behaviour in this population.

Mutual grooming occurred most often when the horses were moulting in the spring and autumn, and focussed on the withers, an area inaccessible to a horse with its own teeth or hooves. Stand resting together was observed most often during the summer and its primary function is likely to be fly relief. However these behaviours were relatively rare. With increasing population size, which may lead to increased aggression, there may also be a concomitant increase in associative behaviours to alleviate social stress. Future research would show whether there is a positive relationship between social factors and associative behaviours as the population grows, which would be consistent with the hypothesis that mutual grooming has a basic hygienic function, but can assume a social significance.

Stallion marking behaviour fell in to two categories: marking of stud piles, and marking of mare eliminations. Other studies have not differentiated between the two types of marking, however this study showed that the behaviours used to mark these two stimuli were discrete and appeared to have different functions. It appears that both types of marking enable stallions to make decisions of the cost of a confrontation based on the chemical information contained in the faeces or urine and previous knowledge of the marker.

Stallions marked stud piles by sniffing them, defecating on the pile, then sniffing again. Stud piles were found in areas that would have a relatively high visual impact, such as on roads and paths and ridges. As all stallions, including bachelors, mark stud piles when they pass it is likely that they provide information of other stallions that have used that area, and so will enable the harems to avoid each other. They will also enable stallions to become familiar with the smell of potential rivals, and may also provide orientation points in the landscape.

Mare eliminations were mostly marked with urine, and were only sniffed before marking. Not all mare eliminations were marked, and there is no evidence that the stallion was attempting to alter or hide the smell. However, as most marking of mare eliminations took place during the breeding season, it is likely that the stallion was signalling his consortship of the mare. A stallion coming across this mark can then judge the costs and benefits of fighting for the mare based on the information

contained chemically within the urine and past experience of confrontations with the consorting stallion.

There was no correlation between length of time since release or group size and frequency of vigilance, but larger groups that had been released for longer tended to spend more time grazing than smaller, more recently released harems, which is consistent with the many eyes hypothesis. Older horses that had been longest in the harem and were higher ranking tended to be the most vigilant individuals. In addition to scanning for predators, vigilance appeared to serve other functions such as searching for social cues and looking for food patches. Most vigilance was observed in the spring and autumn, which was when most wolf predation occurred, and the landscape and 'unknown stimuli' (possibly also the landscape, or else movement, scent, sound or an animal undetected by the observer) were scanned most frequently. This peak of vigilance in the spring also coincided with the breeding season. As a great deal of vigilance was directed at other group members, and least vigilance occurred at dawn and dusk, the time when predators are most likely to be active, it appears that most vigilance was for social reasons.

There were few biting flies at HNP and so all effects of flies must be due to their annoyance, rather than the pain of a bite. Flies were most abundant by the stream and in the lower parts of the valleys. Fly numbers increased with the temperature, but appeared most abundant around 25°C and when the wind was not too strong (about 3 km $hour^{-1}$). The horses moved up to rocks to shelter from flies during the heat of the day. Although there was no difference in temperature between the grazing places and resting places, and the comfort behaviour level was higher, stand resting on bare ground by rocks must have provided some relief from flies. Use of the woodland can only have been due to a need for shade as there were more flies, and the temperature was higher than at the resting areas.

Most flies belonged to the family Muscidae, and Calliphoridae were also common. The main effect of these flies on horses will be annoyance, since they consume facial excretions, and as vectors of disease and infection. Tabanidae appeared rare, but due to the number of eggs and larvae observed, Gasterophilidae must be relatively common. The apparent scarcity of these families could be due to the sampling methods used. Concerted trapping for these families would be useful so that the extent of their effect on the horses could be quantified. Other internal parasites of the horses should also be examined, since these will also have an effect on the condition of the

animals. Small populations are vulnerable to outbreaks of disease (Saltz *et al.*, 2000), so a greater knowledge of the abundance of ticks, especially *Dermacentor nutalli*, the vector of babesia, and other potential equine diseases is important.

6.2 Management and future concerns

There is little evidence that any ability of the Przewalski horses to survive in the wild has been lost through the generations in captivity. Although there has been high mortality of horses within the first year of release, the survival of horses born in HNP has been good (of 115 horses born between 1993 and 2001 57% are still alive). The population continues to grow despite the high mortality from babesia of horses brought to Mongolia in 1998. It has therefore been effectively self-sustaining for over five years. Thus, to date, the reintroduction of the Przewalski horse to HNP has been a success.

The main problem likely to affect this small population is the lack of genetic diversity. Due to the bottlenecks imposed on Przewalski horses by the 13 founders of the captive population and few horses surviving the Second World War, inbreeding is a problem in any Przewalski horse population. The HNP horses were chosen for release based on their low inbreeding coefficients in an attempt to minimise any deleterious effects. However, the effective population size (N_e) of the population has been reduced because only three stallions produced all surviving offspring for the first four years of the reintroduction (21 foals between 1993 and 1997). The same effect was observed in a reintroduced population of Asiatic wild asses where one stallion monopolised all the mares (Saltz *et al.*, 2000). In this population it was thought that the problem might be ameliorated with an increase in male turnover and female use of several territories. Hopefully the same will be true at HNP. An increased male turnover is already apparent at HNP, although the males becoming harem stallions are offspring of the original three. The parallel with increased female use of territories is the presence of more, but smaller, harems which is also being seen.

There is a high potential for further inbreeding as the young horses of the three stallions establish harems containing full or half siblings. Other studies have suggested that familiarity between fathers and their offspring should prevent breeding among them (Berger & Cunningham, 1987), and it is possible that a similar mechanism will prevent breeding between siblings. If this is true then there is a further problem of

horses dispersing from the park in an attempt to find unfamiliar animals with which to mate.

Hybridisation with domestic horses is a threat that will hang over any reintroduction of Przewalski horses to Mongolia; domestic horses are essential for the way of life of the local people. The population at HNP is particularly at threat as the park borders a migration corridor for nomads. The park's proximity to Ulaan Baatar means that the surrounding steppe is under pressure as increasing numbers of nomads move towards Ulaan Baatar in an attempt to get better prices for their animals in the current financial depression of the country. This situation also means that Przewalski horses should not be allowed to disperse, or set up home ranges, outside the park boundaries. To date there has been one possible case of a hybrid being born, although its parentage is contested. During this study there were no cases of hybridisation, although a bachelor stallion briefly joined a group of domestic horses. It is likely that the different species will remain apart; at Askania Nova in the Ukraine several species of equid are kept in the same pasture and have few interactions. However it is important that a management plan is established to deal with the occurrence of any hybrid offspring. Paternity testing of all foals is currently underway at HNP (Bouman, 2001), and testing for hybridisation should also be routinely done, due to the possibility of sneak matings. If a hybrid is detected in a harem it should either be sterilised and returned to its natal harem or else destroyed. If the mother of the hybrid belongs to a local person then it should at least be ensured that the hybrid never joins the Przewalski population.

Disease and environmental factors such as drought and harsh winters pose the greatest threats to a small population. It is impossible to control for the weather, but research can be conducted on diseases affecting the horses. Some of this research is already being carried out at Tachyn Tal (Walzer *et al.*, 2000). The main diseases that have had an impact on the population at both reintroduction sites are babesia (piroplasmosis) (Ruegg *et al.*, 2002) and strangles (beta haemolytic streptococcus infection) (Walzer *et al.*, 2001), both of which can be treated if diagnosed in time. The presence of a huge number of domestic horses around the release sites mean that the risk of disease transmission is high. It is vital that any outbreaks of disease should be recognised immediately and treated if thought necessary.

A key issue for the survival of the released population is the carrying capacity of HNP for Przewalski horses. There was a similar horse density at HNP as observed in feral horse populations in the western USA, and at current levels the population is

well below the carrying capacity of the park. Although a figure of 500 horses seems feasible based on the total area of the park (570 km^2), the actual area suitable for colonisation by horses is less, due to the topography and availability of water. In the western section of HNP there are streams in most valleys, but in the east (c. 144 km^2) there are only three ephemeral streams. The presence of nutritious vegetation will also affect the spread of horses through the park.

Rather than using total area, a more suitable prediction of the number of harems able to be supported by HNP could be produced from a model containing factors essential to the horses in every home range. From this study these factors appear to be the presence of good quality vegetation, particularly Lowland steppe and Tussock grassland, a reliable water source, and places for resting both by rocks near ridges and among trees. The limited presence of these factors will mean that the actual number of horses able to be supported at HNP is likely to be well below the proposed 500.

The potential population growth will also need to be factored in to this model. The current growth rate is 10% (Bouman, 2001), which is less than some populations of feral horses, in which growth rates of 18% have been recorded (Garrott & Taylor, 1990). On average, only 39% of mares had a foal between 1998 and 2000. Currently the identity of each individual is known and it would be useful if knowledge of each animal was maintained.

Although overlap occurs among the harems' home ranges and core areas, it is not extensive and harems appear to avoid each other and establish home ranges in separate valleys. As the population increases it is likely that overlap will increase. However if this does not occur, harems will soon begin to set up home ranges on the periphery and outside the park, although access to water will ultimately define where the ranges are situated. It is important that home ranges continue to be monitored so that future movements of the horses can be predicted. As the Przewalski horse population grows there will be more pressure on the vegetation, especially on the vegetation classes of the valleys that are most selected by the horses. The vegetation and the horses use of it must continue to be monitored to provide an early warning of any evidence of overgrazing.

When the horse population reaches the carrying capacity of the park it will need to be controlled, both to prevent overgrazing and dispersal from the area. Przewalski horses born in Mongolia will be acclimatised to the rigorous conditions there, so HNP could provide an important source of horses for future reintroductions in other areas of

Mongolia. If horses are not removed the population will need to be controlled in other ways. Due to the expense of the reintroduction, and its success, it would seem a waste to shoot horses or remove them to zoos, so contraception would be a good alternative. In a model of feral horses in the Pryor Mountains of America, Gross (2000) found that contraception was better for controlling the population than removal of animals, which resulted in a wide fluctuation of population size. Importantly for HNP, Gross (2000) also found that less genetic variation was lost if random-aged or young animals were treated with contraceptives rather than older animals.

The reintroduced Przewalski horses appear to act in a way very similar to feral domestic horses: they have a similar social structure, home range and habitat use. Studies of feral horses can therefore provide guidelines for the management of this population, but studies of this new population can also provide information for the management of feral horses through information on the mechanics of dispersal of horses and harem formation.

6.3 Applications for other reintroductions

Results of this study have several applications for future reintroductions. The key finding was that animals showed a strong fidelity to their release site, only gradually moving away from the enclosure, although remaining in the same valley. In this population this has resulted in overlap of home ranges and core areas and a single valley being used by a large proportion of the population. The horses that were brought to HNP in 2000 have been placed in acclimatisation enclosures in the eastern part of the park, so this may result in a more spread out population. However two of these enclosures were built within sight of each other, which has resulted in stallions jumping out of their enclosures and suffering injuries in fights. Future reintroductions should ensure that enclosures are visually separated and that only one release is performed from each enclosure.

Releases of horses with an acclimatisation period of less than a year have not been successful, with high levels of mortality observed. Of the harem given a hard release straight from the travelling crates (Turgen's), and the two harems released after an acclimatisation period of five months (Mark's and Bohemian's harems) (n = 17 horses) only four horses survived. It is therefore important that animals have experience of each season of the year before their release. This will enable them to adjust to the weather conditions, and also learn how to find food and shelter while

being in a more easily managed situation. Longer acclimatisation times are also likely to allow the horses to become infected with babesia, and develop immunity without suffering the increased effects of the disease from the stress of free-living.

The importance of releasing an even sex ratio of animals has been demonstrated at HNP. Although an equal number of mares and stallions were imported to the park, until 2001 the bachelor stallions were kept in an enclosure as a source to replace harem stallions. This resulted in three stallions fathering the founder offspring of the population, which will affect the inbreeding coefficient of the population in the future. A similar problem was encountered with the reintroduction of the Asiatic wild ass in Israel, with one stallion monopolising the mares (Saltz *et al.*, 2000). In this study they also showed how stallions with familiarity of the area had an advantage over released animals. Future reintroductions may therefore benefit by simultaneously releasing a number of established harem groups, plus a group of bachelor males who can learn the environment and ultimately challenge the harem stallions. However, the costs and benefits have to be balanced since there may be lower reproductive success in the event of high male turnover (Berger, 1983a).

The reintroduction of the Przewalski horse to HNP appears to have been successful, since the population is surviving the conditions in Mongolia and continuing to grow. Lessons learnt from this reintroduction can hopefully benefit others, but study of this population in the future will provide important information on the biology of this species, and more generally, on factors affecting small and newly released populations.

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Appendix I. Composition of free-ranging harems at HNP.

Names in brackets indicate which harem the horse came from: Pat=Patron, Kha=Khaan, Par=Paritet, Bay=Bayan, Mar=Margad, Boh=Bohemian, Mark=Mark, Manl=Manlai, Mang=Mangir. Names in brackets with years indicate the mother and year of birth. Horses that do not appear along a row dispersed, or died. Except in the case of foals the date of death is given. An asterisk indicates residence in a harem of less than six months.

	1994		1995		1996		1997		1998		1999		2000	
Harem	Name	Sex	Name	Sex	Name	Sex	Name	Sex	Name	Sex	Name	Sex	Name	Sex
Khaan	Khaan	m	Khaan	m	Khaan	m	Khaan	m	Khaan	m	Khaan	m		
	Vetochka	f	Vetochka	f	Vetochka	f	Vetochka	f	Vetochka	f				
	Svetlaya	f	Svetlaya	f	Svetlaya	f	Svetlaya	f	Svetlaya	f	Svetlaya	f		
	Riska	f	Riska	f	Riska	f	Riska	f	Riska	f				
	Belka	f	Belka	f	Belka	f	Belka	f	Belka	f	Belka	f		
					Shuurga (Par)	f	Shuurga	f	Shuurga	f	Shuurga	f		
							Naidvar (Par)	f	Naidvar	f				
			Ireedui (Pat)	f	Ireedui	f	Ireedui	f	Ireedui	f	Ireedui*	f		
							Tsetseg (Pat)	f	Tsetseg	f				
	Manlai (Bel 93)	m	Manlai (Bel 93)	m										
	Amar (Vet 94)	m	Amar (Vet 94)	m	Amar (Vet 94)	m	Amar (Vet 94)*	m						
	Tuul (Bel 94)	f	Tuul (Bel 94)	f										
	Sve 94	f	Oesoech (Vet 95)	f	Oesoech (Vet 95)*	f								
	Ris 94	m	Sve 95	m	Delgarekh (Bel 96)	f	Delgarekh (Bel 96)	f	Delgarekh (Bel 96)*	f				
			Ris 95	m	Chotzj (Ris 96)	f	Chotzj (Ris 96)	f	Chotzj (Ris 96)	f				
					Adzargal (Vet 96)	m	Adzargal (Vet 96)	m	Adzargal (Vet 96)*	m				
					Sve 96	m	Evsel (Sve 97)	m	Evsel (Sve 97)	m				
							Balmoral (Shu 97)	m	Balmoral (Shu 97)	m	Balmoral (Shu 97) *	m		
							Bernard (Ris 97)	m	Bernard (Ris 97)	m				
							Ire 97	f	Naadam (Ris 98)	f				
							Bel 97	f	Tushig (Nai 98)	m				
									Selenge (Ire 98)	m	Selenge (Ire 98)*	m		
									Vet 98	f	Sudi (Bel 99)	f		
									Shu 98	m	Munkh-Arivijk (Sve 99	m		
									Sve 98	f	Shu 99	f		
									Bel 98	m	Ire 99	f		

	1994		1995		1996		1997		1998		1999		2000	
Patron	Patron	m	Patron	m	Patron	m	Patron	m	Patron	m	Patron	m	Patron	m
	Altan	f	Altan	f	Altan	f	Altan	f	Altan	f	Altan	f	Altan	f
	Tanaa	f	Tanaa	f	Tanaa	f	Tanaa	f	Tanaa	f	Tanaa	f	Tanaa	f
	Zaluu	f	Zaluu	f	Zaluu	f	Zaluu	f	Zaluu	f	Zaluu	f	Zaluu	f
	Hatan	f	Hatan	f	Hatan	f	Hatan	f	Hatan	f	Hatan	f	Hatan	f
	Hjalgana	f	Hjalgana (d. May 95	f										
					Dzargal (Enc 2)	f	Dzargal	f	Dzargal	f	Dzargal	f	Dzargal	f
					Asgaa (Enc 2)	f	Asgaa	f	Asgaa	f	Asgaa	f	Asgaa	f
					Undraga (Enc 2)	f	Undraga	f	Undraga	f	Undraga	f	Undraga	f
					Agaar (Enc 2)	f	Agaar	f	Agaar	f	Agaar	f	Agaar	f
					Sharga (Enc 1)	f								
							Tuul (Kha)	f	Tuul	f	Tuul	f	Tuul	f
	Goio (Hat 94)	m	Goio (Hat 94)	m	Goio (Hat 94)	m								
	Ireedui (Hja 94)	f												
	Mangir (Taa 94)	m												
	Margad (Alt 94)	m	Margad (Alt 94)	m	Margad (Alt 94)*	m								
	Khuskhan (Zal 94	f	Khuskhan (Zal 94)	f										
			Tsetseg (Tan 95)	f	Tsetseg (Tan 95)	f								
			Narstai (Hat 95)	m	Narstai (Hat 95)	m	Narstai (Hat 95)	m						
			Hja 95	f	Zigmee (Tan 96)	f	Zigmee (Tan 96)	f	Zigmee (Tan 96)*	f				
					Khangai (Zal 96)	f	Khangai (Zal 96)	f						
					Alt 96	f	Temuulen (Hat 97)	m	Temuulen (Hat 97)	m				
					Hat 96		Aga 97		Shiliin Bod (Hat 98)	m	Shiliin Bod (Hat 98)	m	Shiliin Bod (Hat 98)	m
									Zost Bor (Tuu 98)	m	Zost Bor (Tuu 98)	m		
									Turgen (Aga 98)	m	Turgen (Aga 98)	m		
									Khereed (Tan 98)	f	Khereed (Tan 98)	f	Khereed (Tan 98)	f
									Khiimor (Zal 98)	f	Khiimor (Zal 98)	f	Khiimor (Zal 98)	f
									Dza 98	f	Munkhsanaa (Dza 99)	m	Munkhsanaa (Dza 99)	m
									Und 98	f	Janna (Tan 99)	f	Janna (Tan 99)	f
											Bambar (Hat 99)	m	Bambar (Hat 99)	m
											Aga 99	f	Tuu 00	m
											Und 99	f	Aga 00	m
													Taa 00	f
													Zal 00	m
													Hat 00	m
													Dza 00 (d. May 00)	

1994	1995		1996		1997		1998		1999		2000	
Paritet	Paritet	m	Paritet	m	Paritet	m	Paritet	m	Paritet	m	Paritet	m
	Shuurga	f										
	Naidvar	f	Naidvar	f					Naidvar	f	Naidvar	f
	Tengis	f	Tengis	f	Tengis	f	Tengis	f	Tengis	f	Tengis	f
	Buyana	f	Buyana	f	Buyana	f	Buyana	f	Buyana	f	Buyana	f
	Boroo	f	Boroo	f	Boroo	f	Boroo	f	Boroo	f	Boroo	f
	Uvul	f	Uvul	f	Uvul	f	Uvul	f	Uvul	f	Uvul	f
			Khuskhan (Pat)	f	Khuskhan	f	Khuskhan	f	Khuskhan	f	Khuskhan	f
									Ayunga (Boh)	f	Ayunga	f
					Ov (Khu 97)	m	Ov (Khu 97)	m	Ov (Khu 97)	m	Ov (Khu 97)	m
	Shu 95	m	Bor 96	f	Ten 97	m	Flicka (Ten 98)	f	Flicka (Ten 98)	f	Flicka (Ten 98)	f
			Ten 96	f	Buy 97	m	Khu 98	m	Tushig (Nai 98)	m	Tushig (Nai 98)	m
							Bor 98	f	Tuvchi (Khu 99)	f	Tuvchi (Khu 99)	f
							Uvu 98	f	Chonokhuu (Ten 99)	f	Chonokhuu (Ten 99)	f
									Julian (Bor 99)	f	Julian (Bor 99)	f
									Uvu 99	m	Khu 00	f
									Nai 99	m	Ten 00	

Turgen			Turgen	m	Turgen (d. Apr 97)	m
			Meta	f	Meta	f
			Inge	f	Sharga (Pat)	f
			Maize	f		
			Ikh Gobi (Met 96)	m		

1994	1995	1996	1997	1998		1999		2000	
Bayan				Bayan	m	Bayan	m	Bayan	m
				Badmaa	f	Badmaa	f	Badmaa	f
				Meta (Tur)	f				
				Ajarchan	f	Ajarchan	f	Ajarchan	f
				Sharga (Tur)	f	Sharga	f	Sharga	f
				Sergelen	f	Sergelen	f		
						Zigmee (Pat)	f	Zigmee	f
						Delgerekh (Pat)	f	Delgerekh	f
				Marcview (Aja 98)	m	Marcview (Aja 98)	m	Marcview (Aja 98)	m
				Met 98	f	Ingrid (Bad 99)	f	Ingrid (Bad 99)	f
						Glori (Sha 99)	f	Glori (Sha 99)	f
								Bad 00	f
								Zig 00	f
								Del 00	f
Ares				Ares	m	Ares	m	Ares	m
				Tsagaan	f	Tsagaan	f	Tsagaan	f
				Ayush	f	Ayush	f	Ayush	f
				Khalioen	f	Khalioen	f	Khalioen	f
				Zeerd	f	Zeerd	f	Zeerd	f
				Caborg	f	Caborg (d. Sep 99)	f	Caborg (d. Sep 99)	f
				Aoshka (Tsa 98)	m	Aoshka (Tsa 98)	m	Aoshka (Tsa 98)	m
				Enkhriima (Ayu 98)	f	Enkhriima (Ayu 98)	f	Enkhriima (Ayu 98)	f
				Kha 98	m	Azin Od (Zee 99)	m	Azin Od (Zee 99)	m
								Ayu 00	m
								Kha 00	m
								Tsa 00	m
Bohemian				Bohemian	m	Bohemian	m		
				Jiruken	f	Jiruken (d. Feb 99)	f		
				Byambaa	f	Byambaa (d. Apr 99)	f		
				Gunj	f	Gunj (d. Mar 99)	f		
				Ayunga	f	Ayunga*	f		
				Argun	f	Argun (d. Jan 99)	f		
Mark				Mark (d. Dec 98)	m				
				Kharzaga	f				
				Ulziima	f				
				Suvd (d. Apr 99)	f				
				Naran (d. Jan 99)	f				
				Ukhaa	f				
				Bajalag	f				

	1994	1995	1996	1997	1998	1999		2000	
Margad						Margad	m	Margad	m
						Shuurga (Kha)	f	Shuurga	f
						Ireedui (Kha)	f	Ireedui	f
						Riska (Kha)	f	Riska	f
						Tsetseg (Kha)	f	Tsetseg	f
						Chotzj (Kha)	f	Chotzj	f
						Kharzaga (Manl)	f	Kharzaga	f
								Sergelen (Bay)	f
						Vetochka * (Kha)	f		
						Svetlaya * (Kha)	f		
						Delgerekh * (Manl)	f		
						Zigmee * (Manl)	f		
						Evsel (Kha)	f	Evsel	f
						Naadam (Kha)	f	Naadam	f
						Selenge (Kha)	m	Selenge	m
						Dagina (Tse 99)	f	Dagina (Tse 99)	f
						Vet 99	f	Ris 00	m
								Ire 00	f
								Kha 00	f
Manlai						Manlai	m		
						Kharzaga (Mark)*	f		
						Bajalag (d. Apr 99)	f		
						Ukhaa (d. Apr 99)	f		
						Ulziima (d. Apr 99)	f		
						Suvd (d. Apr 99)	f		
						Naran (d. Jan 99)	f		
						Delgerekh*	f		
						Zigmee *	f		
Mangir						Mangir	m	Mangir	m
						Belka (Kha)	f	Belka (Kha)	f
						Svetlaya (Mar)	f	Svetlaya (Mar)	f
						Vetochka (Mar)	f	Vetochka (Mar)	f
						Bel 99	f	Bel 99	f
						Sve 99	m	Sve 99	m
								Bel 00	f

1994	1995		1996		1997		1998		1999		2000	
Bachelor	Ireedui*	f										
	Manlai	m	Manlai	m	Manlai	m	Manlai	m	Manlai*	m		
			Tuul	f	Tuul*	f						
			Amgalan (Enc 3)	m	Amgalan	m						
			Uliral (Enc 2)	m	Uliral	m	Uliral (d. Apr 98)	m				
			Mangir	m	Mangir	m	Mangir	m	Mangir*	m		
			Oesoech*		Goio	m	Goio	m	Goio	m	Goio	m
					Margad	m	Margad	m	Margad*	m		
					Oesoech	f	Amar (to Enc 3)	m				
					Amar*	m	Narstai	m	Narstai	m	Narstai	m
							Delgarekh*	f				
							Khangai	m	Khangai	m	Khangai	m
							Oesoech (d. Apr. 98)	f	Adzargal	m	Adzargal	m
									Temuujen	m	Temuujen	m
									Balmoral	m	Balmoral	m
									Bernard	m	Bernard	m
									Khaan (to Enc 1)	m		
											Turgen	m
											Zost Bor	m

Appendix II. Sampling sessions and their division into standard days.
The length of each day is shown in hours. Sampling sessions below the total were not used in analyses where standard days were used as replicates.

a) Paritet's harem

Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
1998	1	11.6.98	700	1400	26.6.98	1340	1700	
					28.6.98	1950	2130	16.2
	2	29.6.98	550	1400	30.6.98	1440	2200	15.5
	3	16.7.98	720	1400	17.7.98	1430	2200	14.1
	4	28.7.98	620	1400	27.7.98	1620	2000	11.2
	5	29.8.98	630	1400	31.8.98	1440	2100	14.1
							Total:	71.1
					6.10.98	1350	1830	

Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
1999	1	3.5.99	600	1350	22.4.99	1410	1800	11.6
	2	17.5.99	530	1350	4.5.99	1400	1900	12.3
	3	31.5.99	500	1400	28.5.99	1420	1900	13.3
	4	14.6.99	500	1400	15.6.99	1300	1640	
					16.6.99	1710	2100	16.1
	5	5.7.99	430	1350	14.7.99	1410	1600	
					19.7.99	1600	2100	16.1
	6	19.7.99	430	1400	20.7.99	1420	2100	16.1
	7	6.8.99	520	1200	16.8.99	1330	2000	13.3
	8	23.8.99	600	1400	24.8.99	1340	2000	14.6
	9	17.9.99	620	1230	24.9.99	1300	1910	12.4
	10	20.9.99	610	1400	21.9.99	1400	1910	13
	11	8.10.99	630	1400	14.10.99	1400	1550	
					20.10.99	1550	1800	13.5
	12	18.10.99	700	1400	19.10.99	1330	1800	11.5
	13	1.11.99	740	1400	5.11.99	1320	1720	10.3
	14	4.11.99	750	1320	4.11.99	1340	1720	9.5
							Total:	183.6
		2.8.99	530	1400				

Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
2000	1	9.5.00	540	1400	11.5.00	1340	2000	14.6
	2	18.5.00	540	1310	17.5.00	1310	2030	15.1
	3	24.5.00	540	1440	23.5.00	1440	2030	14.8
	4	23.6.00	600	1350	21.6.00	1400	2030	14.3
							Total:	58.8

b) Bayan's harem

Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
1998	1	5.6.98	930	1330	19.6.98	1540	1840	7
	2	15.6.98	545	1400	25.6.98	1500	1720	10.55
	3	6.7.98	640	1400	7.7.98	1350	2200	15.7
	4	31.7.98	1010	1110	30.7.98	1340	2100	8.6
	5	17.8.98	700	1340	18.8.98	1430	1950	11.9
	6	25.9.98	1040	1430	30.9.98	1440	1610	5.5
							Total:	59.25

Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
1999	1	1.5.99	920	1320	30.4.99	1340	1800	7.3
	2	13.5.99	730	1350	25.6.99	1350	2000	12.5
	3	28.6.99	700	1100	29.6.99	1500	2000	
		7.7.99	1200	1500				12
	4	15.7.99	740	1400	23.4.99	1510	1610	
					16.7.99	1630	2000	10.8
	5	22.7.99	450	640				
		26.7.99	930	1400	27.7.99	1410	2000	13.1
	6	18.8.99	700	1300	10.8.99	1400	2000	12
	7	8.9.99	800	1400	16.9.99	1420	1930	11.2
	8	28.9.99	900	1120	27.9.99	1640	1730	3.3
	9	7.10.99	830	1400	15.10.99	1430	1800	9
	10	26.10.99	800	1400	26.10.99	1410	1800	10
							Total:	101.2

Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
2000	1	16.5.00	640	840				
		19.5.00	830	1330	15.5.00	1340	2030	14
	2	26.5.00	540	1400	5.6.00	1700	2000	
					19.6.00	1400	1700	14.3
	3	26.6.00	720				1930	12.2
							Total:	40.5
					22.6.00	1330	1630	

c) Margad's harem

Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
1999	1	10.5.99	620	1350	11.5.99	1340	1810	11
	2	7.6.99	530	1350	25.5.99	1340	1920	14.3
	3	1.7.99	710	1330	2.7.99	1510	2050	12.2
	4	22.7.99	500	1050	23.7.99	1430	2100	12.3
	5	14.8.99	500	1400	15.8.99	1440	2000	14.3
	6	28.8.99	620	1400	7.9.99	1340	1950	14
	7	26.9.99	650	1400	25.9.99	1400	1900	12.2
	8	21.10.99	800	1400	17.10.99	1340	1800	9.3
	9	27.10.99	800	1330	23.10.99	1340	1800	8.8
							Total:	108.4
		3.6.99	750	1330				

Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
2000	1	13.5.00	530	1330	12.5.00	1330	1950	14.3
	2	25.5.00	530	1400	22.5.00	1400	2030	15
	3	1.6.00	530	1400	30.6.00	1400	2000	14.5
							Total:	43.8

d) Khaan's harem

Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
1998	1	8.6.98	620	1400	9.6.98	1400	2200	15.6
	2	18.6.98	630	1400	17.6.98	1630	1820	9.5
	3	2.7.98	610	1400	14.7.98	1420	1600	
					3.8.98	1720	2030	12.6
	4	6.8.98	630	1200	14.8.98	1420	2100	12.1
	5	3.9.98	650	930	15.9.98	1500	2000	
		4.9.98	1020	1300				
					4.10.98	1400	1700	10.2
							Total:	60

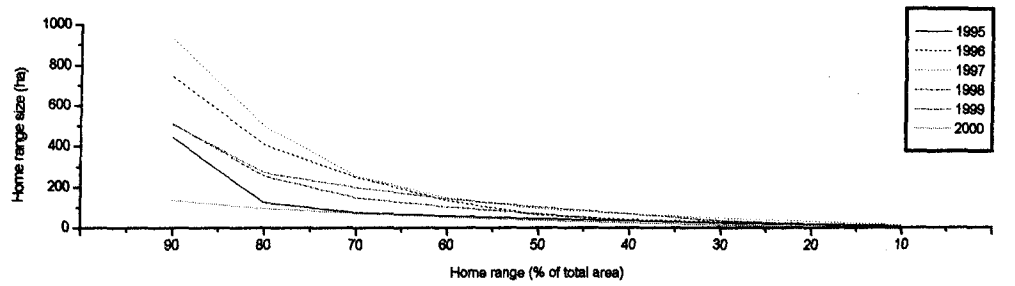
Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
1999	1	26.4.99	700	1100	27.4.99	1500	1900	8
	2	24.5.99	700	1500	4.6.99	1530	1800	10.5
	3	27.5.99	530	1230	8.6.99	1430	2030	13
							Total:	31.5

e) Ares' harem

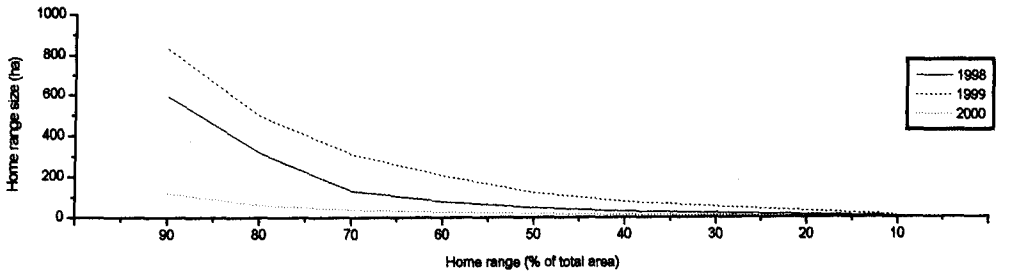
Year	Standard day	Date	Start	Stop	Date	Start	Stop	Total hours
1998	1	20.7.98	810	1400	21.7.98	1500	1930	10.3
	2	10.8.98	800	1400	3.8.98	1450	1620	7.5
	3	28.9.98	730	1400	4.8.98	1430	2100	14
	4	8.10.98	850	1400	2.10.98	1400	1800	9.2
							Total:	41

Appendix III. Utilisation curves of the different harems.
Core areas at 80% for all harems in all years.

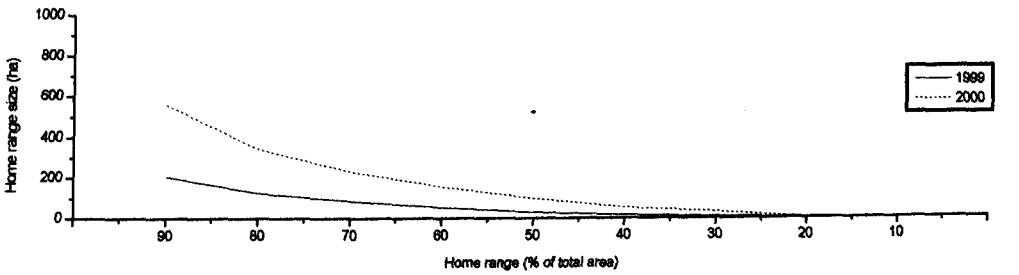
a) Parítet's harem



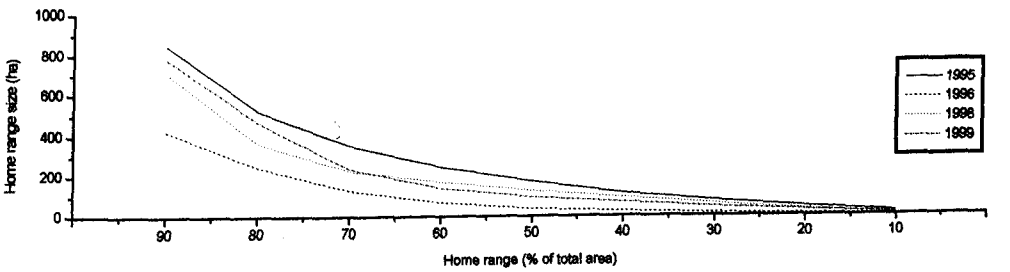
b) Bayan's harem



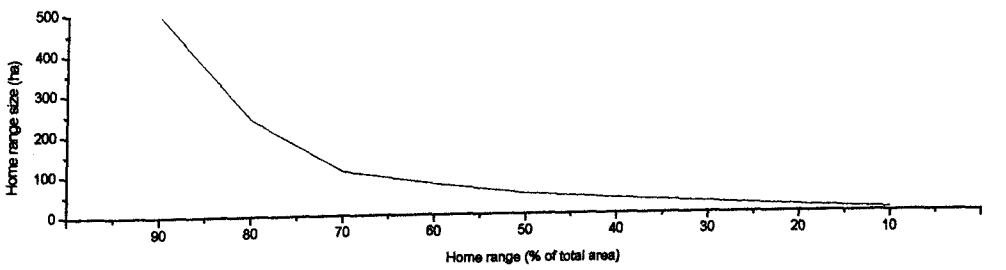
c) Margad's harem



d) Khaan's harem



e) Ares' harem



Appendix IV. Results of Kruskal-Wallis analyses of time budget data of each harem. Differences between the months and hours within each year are shown, and any differences in the behaviour among the years.

Paritet	1998		1999		2000	
	Month	Hour	Month	Hour	Hour	Year
Grazing	H=3.86, df=3, p=0.277	H=90.03, df=16, p=<0.001	H=108.79, df=7, p=<0.001	H=94.54, df=17, p=<0.001	H=140.70, df=23, p=<0.001	H=12.34, df=2, p=0.002
Lying down			H=30.43, df=7, p=<0.001	H=18.17, df=17, p=0.378	H=164.46, df=23, p=<0.001	H=128.65, df=2, p=<0.001
Moving	H=9.37, df=3, p=0.025	H=28.01, df=16, p=0.032	H=14.26, df=7, p=0.047	H=60.92, df=17, p=<0.001	H=38.73, df=23, p=0.021	H=19, df=2, p=<0.001
Standing	H=36.18, df=3, p=0.103	H=18.82, df=16, p=0.278	H=9.72, df=7, p=0.205	H=33.09, df=17, p=0.011	H=31.25, df=23, p=0.117	H=1.75, df=2, p=0.417
Stand resting	H=6.67, df=3, p=0.083	H=149.64, d16, p=<0.001	H=88.58, df=7, p=<0.001	H=149.08, df=17, p=<0.001	H=164.96, df=32, p=<0.001	H=26.79, df=2, p=<0.001

Bayan	1998		1999		2000	
	Month	Hour	Month	Hour	Hour	Year
Grazing	H=11.41, df=4, p=0.022	H=47.08, df=16, p=<0.001	H=119.13, df=6, p=<0.001	H=55.40, df=16, p=<0.001	H=84.80, df=15, p=<0.001	H=22.09, df=2, p=<0.001
Lying down			H=22.83, df=6, p=0.001	H=35.25, df=16, p=0.004		H=4.52, df=2, p=0.104
Moving	H=16.04, df=4, p=0.003	H=12.18, df=16, p=0.731	H=32.84, p=<0.001	H=26.41, df=16. P=0.049	H=42.01, df=15, p=<0.001	H=2, df=2, p=0.368
Standing	H=11.62, df=4, p=0.02	H=22.10, df=16, p=0.140	H=7.84, df=6, p=0.250	H=35.17, df=16, p=0.004	H=14.54, df=15, p=0.485	H=0.29, df=2, p=0.863
Stand resting	H=13.90, df=4, p=0.008	H=14.01, df=16, p=0.001	H=32.78, df=6, p=<0.001	H=77.27, df=16, p=<0.001	H=98.79, df=15, p=<0.001	H=44.74, df=2, p=<0.001

Margad			1999		2000	
			Month	Hour	Hour	Year
Grazing			H=30.70, df=5, p=<0.001	H=35.22, df=16, p=0.004	H=67.09, df=15, p=<0.001	H=2.78, df=1, p=0.096
Lying down			H=17.29, df=5, p=0.004	H=26.62, df=16, p=0.0046	H=21.90, df=15, p=0.110	H=0.01, df=1, p=0.936
Moving			H=17.33, df=5, p=0.004	H=23.74, df=16, p=0.095	H=22.92, df=15, p=0.086	H=5.56, df=1, p=0.018
Standing			H=15.96, df=5, p=0.007	H=22.67, df=16, p=0.123	H=11.32, df=15, p=0.730	H=19.04, df=1, p=<0.001
Stand resting			H=26.43, df=5, p=<0.001	H=92.56, df=16, p=<0.001	H=64.89, df=15, p=<0.001	H=5.54, df=1, p=0.019

Khaan	1998		1999			
	Month	Hour	Month	Hour		Year
Grazing	H=24.38, df=4, p=<0.001	H=119.41, df=16, p=<0.001	H=31.29, df=2, p=<0.001	H=35.64, df=15, p=0.002		H=3.16, df=1, p=0.075
Lying down	H=12.70, df=4, p=0.013	H=25.56, df=16, p=0.061				H=25.56, df=1, p=<0.001
Moving	H=11.36, df=4, p=0.023	H=64.61, df=16, p=<0.001	H=11.43, df=2, p=0.003	H=33.43, df=15, p=0.004		H=39.92, df=1, p=<0.001
Standing	H=18.19, df=4, p=0.001	H=11.10, df=16, p=0.803	H=13.47,df=2, p=0.001	H=30.39, df=15, p=0.011		H=34.05, df=1, p=<0.001
Stand resting	H=37.23, df=4, p=<0.001	H=128.23, df=16, p=<0.001	H=13.26, df=2, p=0.001	H=42.94, df=15, p=<0.011		H=177.57, df=1, p=<0.001

Ares	1998	
	Month	Hour
Grazing	H=4.82, df=3, p=0.185	H=46.17, df=14, p=<0.001
Lying down	H=1.83, df=3, p=0.710	H=8.20, df=14, p=0.879
Moving	H=13.63, df=3, p=0.003	H=30.30, df=14, p=0.007
Standing	H=7077, df=3, p=0.051	H=7.16, df=14, p=0.928
Stand resting	H=25.16, df=3, p=<0.001	H=57.92, df=14, p=<0.001

Appendix V. Amount of time behaviour is synchronous (%)

Mare	Foal	% synchronous
Tengis	Tengis 00	71
Khuskhan	Khuskhan 00	65
Riska	Riska 00	65
Badmaa	Badmaa 00	47
Delgerekh	Delgerekh 00	56
Zigmee	Zigmee 00	60

Mare	Juvenile	% synchronous
Tengis	Tengis 99	86
Boroo	Boroo 99	86
Khuskhan	Khuskhan 99	81
Badmaa	Ingrid	75
Shärgä	Glory	81
Tsetseg	Dagina	88
Tengis	Flicka	85
Naidvar	Tushig	84
Riska	Naadam	76
Ireedui	Selenge	87
Ajarchan	Marcview	89
Khuskhan	Ov	87
Riska	Evsel	71

Siblings		% synchronous
Flicka	Tengis 99	84
Ov	Khuskhan 99	76
Evsel	Naadam	73

Stallion	Harem score	% synchronous
Paritet	0.745	65
Margad	0.750	64
Bayan	0.746	78

Appendix VI. Habitat (vegetation) selection indices.

Results of a chi-square test to test the significance of wi are shown. Blank rows indicate the harem was not observed on that vegetation class. * = a negative lower limit has been changed to 0.000. Results from classes with a sample count of less than 5 must be treated with caution.

a) Paritet

1998

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I											
Tussock grassland	0.111	42	0.214	0.135	0.293	1.929	0.265	1.219	2.639	12.399	<0.0001
Lowland steppe	0.237	68	0.347	0.255	0.438	1.467	0.202	1.080	1.853	10.542	<0.01
Upland steppe											
Shrubland I	0.109	14	0.071	0.022	0.121	0.656	0.090	0.202	1.111	4.133	<0.05
Mountain steppe I	0.214	19	0.097	0.040	0.154	0.453	0.062	0.187	0.719	30.667	<0.0001
Mountain steppe II	0.159	29	0.148	0.080	0.216	0.929	0.128	0.501	1.357	0.199	>0.5
Shrubland II	0.115	8	0.041	0.003	0.079	0.354	0.049	0.024	0.684	27.721	<0.0001
Meadow II											
Woodland	0.055	16	0.082	0.029	0.134	1.482	0.204	0.527	2.438	1.845	<0.5
Scrub											
Total		196					1.0				

1999

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I											
Tussock grassland	0.084	202	0.316	0.265	0.367	3.786	0.493	3.176	4.396	159.939	<0.0001
Lowland steppe	0.307	266	0.416	0.362	0.470	1.354	0.176	1.178	1.530	31.173	<0.0001
Upland steppe	0.003	0	0			0	0				
Shrubland I	0.103	17	0.027	0.009	0.044	0.259	0.034	0.087	0.431	143.100	<0.0001
Mountain steppe I	0.236	100	0.156	0.117	0.196	0.662	0.086	0.494	0.831	30.870	<0.0001
Mountain steppe II	0.112	10	0.016	0.002	0.029	0.140	0.018	0.018	0.261	386.515	<0.0001
Shrubland II	0.116	24	0.038	0.017	0.058	0.325	0.042	0.145	0.505	107.605	<0.0001
Meadow II											
Woodland	0.034	19	0.030	0.011	0.048	0.866	0.113	0.324	1.408	0.468	<0.5
Scrub											
Agricultural area	0.005	1	0.002	0*	0.006	0.291	0.038	0*	1.097	5.942	<0.025
Total		639					1.0				

2000

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I											
Tussock grassland	0.130	188	0.566	0.493	0.639	4.348	0.624	3.787	4.910	257.008	<0.0001
Lowland steppe	0.344	74	0.223	0.161	0.284	0.649	0.093	0.470	0.827	27.950	<0.001
Upland steppe											
Shrubland I	0.080	16	0.048	0.017	0.080	0.605	0.087	0.208	1.003	7.142	<0.01
Mountain steppe I	0.189	7	0.021	0.000	0.042	0.111	0.016	-0.001	0.223	455.804	<0.0001
Mountain steppe II	0.106	36	0.108	0.063	0.154	1.021	0.146	0.589	1.453	0.016	>0.5
Shrubland II	0.140	11	0.033	0.007	0.060	0.237	0.034	0.048	0.426	117.986	<0.0001
Meadow II											
Woodland	0.011	0	0			0	0				
Scrub											
Total		332					1.0				

b) Bayan

1998

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I											
Tussock grassland	0.025	2	0.012	0*	0.036	0.475	0.104	0*	1.412	2.483	<0.5
Lowland steppe	0.014	1	0.006	0*	0.023	0.422	0.093	0*	1.603	1.890	<0.5
Upland steppe	0.209	42	0.253	0.158	0.348	1.213	0.267	0.759	1.668	1.740	<0.5
Shrubland I	0.237	39	0.235	0.142	0.327	0.993	0.219	0.602	1.384	0.002	>0.5
Mountain steppe I	0.407	80	0.482	0.373	0.591	1.184	0.261	0.916	1.452	3.731	<0.1
Mountain steppe II	0.047	2	0.012	0*	0.036	0.256	0.056	0*	0.761	17.124	<0.0001
Shrubland II	0.016	0	0			0	0				
Meadow II											
Woodland	0.007	0	0			0	0				
Scrub	0.019	0	0			0	0				
Rock & stones	0.020	0	0			0	0				
Total		166					1.0				

1999

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I	0.014	24	0.072	0.031	0.112	5.238	0.337	2.292	8.184	16.928	<0.001
Tussock grassland	0.057	8	0.024	0	0.048	0.420	0.027	0	0.840	15.624	<0.001
Lowland steppe	0.120	42	0.126	0.074	0.178	1.052	0.068	0.618	1.486	0.119	>0.5
Upland steppe	0.167	45	0.135	0.081	0.188	0.805	0.052	0.486	1.124	3.051	<0.1
Shrubland I	0.204	128	0.383	0.307	0.459	1.882	0.121	1.509	2.256	45.608	<0.0001
Mountain steppe I	0.196	55	0.165	0.107	0.223	0.841	0.054	0.545	1.137	2.355	<0.5
Mountain steppe II	0.179	18	0.054	0.019	0.089	0.301	0.019	0.104	0.498	102.548	<0.0001
Shrubland II	0.007	4	0.012	-0.005	0.029	1.688	0.109	0*	4.088	0.673	<0.5
Meadow II	0.009	0	0			0	0				
Woodland	0.026	4	0.012	-0.005	0.029	0.465	0.030	0*	1.127	5.347	<0.025
Scrub	0.017	1	0.003	-0.006	0.012	0.180	0.012	0*	0.696	20.680	<0.0001
Rock & stones	0.006	5	0.015	-0.004	0.034	2.648	0.171	0*	6.010	1.966	<0.5
Total		334					1.0				

2000

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I	0.023	16	0.131	0.045	0.217	5.816	0.451	2.007	9.624	12.627	<0.001
Tussock grassland	0.006	0	0			0	0				
Lowland steppe	0.126	33	0.270	0.157	0.384	2.139	0.166	1.245	3.033	12.829	<0.001
Upland steppe	0.070	3	0.025	0*	0.064	0.354	0.027	0*	0.921	10.261	<0.01
Shrubland I	0.205	26	0.213	0.109	0.317	1.039	0.081	0.531	1.547	0.046	>0.5
Mountain steppe I	0.108	7	0.057	0*	0.117	0.529	0.041	0*	1.074	5.895	<0.025
Mountain steppe II	0.365	28	0.230	0.123	0.336	0.628	0.049	0.335	0.921	12.717	<0.001
Shrubland II											
Meadow II	0.016	2	0.016	0*	0.049	1.019	0.079	0*	3.028	0.001	>0.5
Woodland	0.053	5	0.041	0*	0.091	0.767	0.059	0*	1.710	0.482	<0.5
Scrub	0.027	2	0.016	0*	0.049	0.601	0.047	0*	1.786	0.895	<0.5
Total		122					1.0				

c) Margad

1999

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I	0.020	10	0.023	0.003	0.044	1.156	0.138	0.166	2.145	0.186	>0.5
Tussock grassland											
Lowland steppe	0.132	103	0.242	0.185	0.299	1.834	0.219	1.403	2.266	28.109	<0.001
Upland steppe	0.125	55	0.129	0.085	0.174	1.036	0.123	0.679	1.393	0.075	>0.5
Shrubland I	0.342	153	0.359	0.295	0.423	1.052	0.125	0.865	1.238	0.573	<0.5
Mountain steppe I	0.028	22	0.052	0.022	0.081	1.849	0.220	0.797	2.901	4.891	<0.05
Mountain steppe II	0.245	63	0.148	0.101	0.195	0.605	0.072	0.412	0.797	31.574	<0.0001
Shrubland II											
Meadow II	0.011	2	0.005		0.014	0.432	0.051	0*	1.266	3.480	<0.1
Woodland	0.098	18	0.042	0.016	0.069	0.430	0.051	0.158	0.701	33.074	<0.0001
Scrub											
Total		426					1.0				

2000

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I	0.018	1	0.006	0*	0.022	0.337	0.054	0*	1.241	3.888	<0.05
Tussock grassland											
Lowland steppe	0.055	25	0.152	0.076	0.227	2.753	0.438	1.389	4.117	11.945	<0.001
Upland steppe	0.225	42	0.255	0.163	0.346	1.131	0.180	0.726	1.537	0.760	<0.5
Shrubland I	0.431	76	0.461	0.356	0.565	1.069	0.170	0.827	1.311	0.589	<0.5
Mountain steppe I											
Mountain steppe II	0.190	15	0.091	0.031	0.151	0.478	0.076	0.161	0.794	19.742	<0.001
Shrubland II											
Meadow II	0.009	0	0			0	0				
Woodland	0.071	6	0.036	0.000*	0.076	0.510	0.081	0.000*	1.059	5.767	<0.025
Scrub											
Total		165					1.0				

d) Khaan

1998

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I	0.024	61	0.293	0.205	0.382	12.443	0.723	8.680	16.207	72.997	<0.0001
Tussock grassland	0.004	0	0			0	0				
Lowland steppe	0.124	28	0.135	0.068	0.201	1.086	0.063	0.550	1.623	0.204	>0.5
Upland steppe	0.125	20	0.096	0.039	0.154	0.770	0.045	0.310	1.231	1.963	<0.5
Shrubland I	0.297	57	0.274	0.187	0.361	0.922	0.054	0.629	1.214	0.568	<0.5
Mountain steppe I	0.080	0	0			0	0				
Mountain steppe II	0.286	38	0.183	0.107	0.258	0.638	0.037	0.375	0.901	14.952	<0.0001
Shrubland II											
Meadow II	0.014	4	0.019	0*	0.046	1.360	0.079	0*	3.253	0.286	>0.5
Woodland	0.037	0	0			0	0				
Scrub	0.008	0	0			0	0				
Total		208					1.0				

1999

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I	0.003	0	0			0	0				
Tussock grassland	0.089	0	0			0	0				
Lowland steppe	0.220	55	0.458	0.332	0.584	2.081	0.426	1.509	2.653	27.390	<0.001
Upland steppe	0.021	0	0			0	0				
Shrubland I	0.232	29	0.242	0.133	0.350	1.042	0.213	0.576	1.509	0.063	>0.5
Mountain steppe I	0.078	0	0			0	0				
Mountain steppe II	0.217	30	0.250	0.141	0.359	1.153	0.236	0.648	1.658	0.707	<0.5
Shrubland II	0.058	0	0			0	0				
Meadow II											
Woodland	0.082	6	0.050	0*	0.105	0.609	0.125	0*	1.281	2.595	<0.5
Scrub											
Total		120					1.0				

e) Ares

1998

Vegetation class	Proportion of area (p_i i)	Sample count (u_i)	Proportion of use (o_i)	Bonferroni confidence limits of (o_i)		Selection index (w_i)	Standardised index (B_i)	Bonferroni confidence limits of (w_i)		Chi-square of (w_i) with 1 df	
				Lower	Upper			Lower	Upper	X^2	p
Meadow I	0.010	2	0.022	0*	0.065	2.284	0.245	0*	6.709	0.646	<0.5
Tussock grassland											
Lowland steppe	0.063	2	0.022	0*	0.065	0.348	0.037	0*	1.024	7.147	<0.01
Upland steppe	0.156	25	0.275	0.145	0.404	1.762	0.189	0.931	2.593	6.444	<0.025
Shrubland I	0.134	4	0.044	0*	0.103	0.328	0.035	0*	0.772	17.563	<0.0001
Mountain steppe I	0.160	27	0.297	0.164	0.429	1.849	0.198	1.022	2.675	8.093	<0.01
Mountain steppe II	0.382	28	0.308	0.174	0.442	0.805	0.086	0.455	1.156	2.366	<0.5
Shrubland II											
Meadow II	0.017	3	0.033	0*	0.085	1.945	0.209	0*	5.004	0.732	<0.5
Woodland	0.060	0	0			0	0				
Scrub	0.018	0	0			0	0				
Total		91					1.0				

Appendix VII. Results of chi-square tests to show differences in use of different vegetation classes, i.e. whether they were being selected in proportion to their availability.
An asterisk indicates that there was more than one expected value of less than five, so the result should be taken as an indication only.

Harem	1998			1999			2000		
	Chi-square	df	p	Chi-square	df	p	Chi-square	df	p
Paritet	48.88	6	<0.0001	70.68	8	<0.0001	63.36	6	<0.0001
Bayan	27.74	9	<0.01*	90.28	11	<0.0001	65.72	9	<0.0001
Margad				60.73	8	<0.0001	39.85	6	<0.0001
Khaan	130.03	9	<0.0001*	33.73	9	<0.001*			
Ares	37.73	8	<0.0001*						

Appendix VIII. Agonistic behavioural elements according to age and sex (%).

a) Paritet's harem

Behaviour	1998		1999				2000		
	Stallion	Mare	Stallion	Mare	Juvenile	Foal	Stallion	Mare	Juvenile
Bite	0	0	2	0	14	0	0	5	0
Bite threat	0	55	10	61	29	0	8	40	33
Bite threat and chase	0	18	6	8	0	0	8	9	0
Herd	60	0	64	2	0	0	77	9	11
Hind leg kick	0	18	2	10	0	100	0	15	22
Hind leg kick threat	0	0	1	7	29	0	0	7	11
Fore leg strike	0	0	0	0	0	0	2	1	11
Other	40	9	7	12	29	0	2	14	11
Fight	0	0	7	0	0	0	2	0	0

b) Bayan's harem

Behaviour	1998		1999			2000		
	Stallion	Mare	Stallion	Mare	Juvenile	Stallion	Mare	Juvenile
Bite	0	0	5	0	0	0	4	100
Bite threat	0	29	0	52	0	11	33	0
Bite threat and chase	0	14	0	5	0	0	0	0
Herd	56	0	75	0	0	78	0	0
Hind leg kick	0	29	0	19	0	0	29	0
Hind leg kick threat	0	14	0	19	0	0	13	0
Fore leg strike	0	14	0	0	0	0	0	0
Other	44	0	5	5	100	11	21	0
Fight	0	0	15	0	0	0	0	0

c) Margad's harem

Behaviour	1999				2000			
	Stallion	Mare	Juvenile	Foal	Stallion	Mare	Juvenile	Foal
Bite	0	8	0	0	0	3	0	0
Bite threat	0	41	50	0	15	53	0	0
Bite threat and chase	0	6	0	0	0	10	50	0
Herd	64	0	0	0	59	0	0	0
Hind leg kick	5	33	33	0	6	16	50	100
Hind leg kick threat	0	6	17	0	0	9	0	0
Fore leg strike	2	0	0	0	3	0	0	0
Other	4	6	0	100	6	9	0	0
Fight	25	0	0	0	12	0	0	0

d) Khaan's harem

Behaviour	1998				1999		
	Stallion	Mare	Juvenile	Foal	Stallion	Mare	Juvenile
Bite	0	0	0	0	0	0	0
Bite threat	12	29	0	0	0	25	0
Bite threat and chase	24	15	0	0	0	0	0
Herd	47	0	0	0	78	0	0
Hind leg kick	0	21	67	100	0	25	0
Hind leg kick threat	0	6	0	0	0	25	0
Fore leg strike	0	0	0	0	0	0	0
Other	18	21	33	0	6	25	50
Fight	0	0	0	0	17	0	50

e) Ares' harem

Behaviour	1998	
	Stallion	Mare
Bite	0	0
Bite threat	0	40
Bite threat and chase	0	0
Herd	89	0
Hind leg kick	0	20
Hind leg kick threat	0	20
Fore leg strike	0	0
Other	11	20
Fight	0	0

Appendix IX. Dominance hierarchy matrices.

a). Dominance hierarchy matrices of Paritet's harem.

The winner of an interaction is down the side and the loser is along the top of the matrices.

i) 1998

	Sex	*Age*	Paritet	Boroo	Tengis	Khuskhan	Uvul	Buyana	Ov	Total
Paritet	m	9	*	1	1	2	1	1	2	8
Boroo	f	7	0	*	0	1	1	0	0	2
Tengis	f	7	1	0	*	0	0	0	0	1
Khuskhan	f	4	1	0	0	*	1	1	0	3
Uvul	f	6	0	0	0	0	*	2	1	3
Buyana	f	7	1	0	0	0	1	*	0	2
Ov	m	1	0	0	0	0	0	0	*	0
Total			3	1	1	3	4	4	3	19

ii) 1999

	Sex	*Age*	Paritet	Naidvar	Tengis	Boroo	Buyana	Khuskhan	Uvul	Tushig	Ayunga	Ov	Flicka	Total
Paritet	m	10	*	16	10	8	18	8	7	12	20	8	8	115
Naidvar	f	8	3	*	7	6	7	6	4	2	9	5	3	52
Tengis	f	8	0	1	*	4	2	3	0	1	2	2	4	19
Boroo	f	8	4	0	0	*	2	6	6	1	3	3	0	25
Buyana	f	8	1	0	0	0	*	3	0	0	4	5	1	14
Khuskhan	f	5	0	0	0	0	2	*	1	0	1	11	5	20
Uvul	f	7	0	0	0	0	0	0	*	0	2	3	2	7
Tushig	m	1	0	0	0	0	0	0	0	*	0	0	0	0
Ayunga	f	13	0	0	0	0	0	0	0	0	*	2	2	4
Ov	m	2	0	0	0	0	0	0	0	0	0	*	3	3
Flicka	f	1	0	0	0	0	0	0	0	0	0	0	*	0
Total			8	17	17	18	31	26	18	16	41	39	28	259

iii) 2000

	Sex	*Age*	Paritet	Naidvar	Tengis	Boroo	Buyana	Khuskhan	Uvul	Ayunga	Flicka	Tushig	Khu 99	Ov	Ten 99	Bor 99	Total
Paritet	m	11	*	24	24	26	25	30	33	25	23	23	28	35	22	25	343
Naidvar	f	9	0	*	5	5	6	6	3	3	6	5	4	9	3	3	58
Tengis	f	9	1	1	*	1	2	3	1	6	3	2	1	3	3	1	28
Boroo	f	9	0	0	0	*	2	0	0	2	0	0	0	5	0	0	9
Buyana	f	9	3	0	0	0	*	5	1	6	0	0	2	15	1	1	34
Khuskhan	f	6	2	0	0	0	0	*	2	0	2	0	3	9	0	2	20
Uvul	f	8	1	0	0	0	0	0	*	0	1	0	1	4	0	0	7
Ayunga	f	14	1	0	0	0	0	0	0	*	5	0	0	0	1	0	7
Flicka	f	2	0	0	0	0	0	0	0	0	*	1	0	0	0	0	1
Tushig	m	2	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0
Khu 99	f	1	0	0	0	0	0	0	0	0	0	0	*	0	0	1	1
Ov	m	3	0	0	0	0	0	2	0	0	0	0	0	*	1	0	3
Ten 99	f	1	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0
Bor 99	f	1	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0
Total			8	25	29	32	35	46	40	42	40	31	39	80	31	33	511

b). Dominance hierarchy matrices of Bayan's harem.
The winner of an interaction is down the side and the loser is along the top of the matrices.
Bold and italic cells indicate inconsistencies (a circular triad in the hierarchy). In 1999 there is an inconsistency between Ajarchan and Sergelen, and in 2000 there is an inconsistency between Ajarchan and Sharga.

i) 1998

	Sex	*Age*	Badmaa	Bayan	Meta	Ajarchan	Sergelen	Sharga	Total
Badmaa	f	6	*	2	0	0	0	0	2
Bayan	m	9	1	*	2	1	4	1	9
Meta	f	16	0	0	*	0	0	1	1
Ajarchan	f	5	0	0	0	*	0	1	1
Sergelen	f	4	0	2	0	0	*	0	2
Sharga	f	4	0	0	0	0	0	*	0
Total			1	4	2	1	4	3	15

ii) 1999

	Sex	*Age*	Sergelen	Bayan	Badmaa	Ajarchan	Sharga	Marcview	Zigmee	Delgerekh	Total
Sergelen	f	5	*	1	0	***0***	4	0	2	0	7
Bayan	m	10	0	*	6	8	5	5	5	4	33
Badmaa	f	7	0	0	*	1	0	1	0	1	3
Ajarchan	f	6	***1***	0	0	*	0	0	0	1	2
Sharga	f	5	1	0	0	0	*	0	1	2	4
Marcview	m	1	0	0	0	0	0	*	0	0	0
Zigmee	f	3	0	1	0	0	0	0	*	0	1
Delgerekh	f	3	0	0	0	0	0	0	0	*	0
Total			2	2	6	9	9	6	8	8	50

iii) Alternate ranking for mares in 1999 without inconsistencies.

	Badmaa	Ajarchan	Sergelen	Sharga	Zigmee	Delgerekh	Total
Badmaa	*	1	0	0	0	1	2
Ajarchan	0	*	1	0	0	1	2
Sergelen	0	0	*	4	2	0	6
Sharga	0	0	1	*	1	2	4
Zigmee	0	0	0	0	*	0	0
Delgerekh	0	0	0	0	0	*	0
Total	0	1	2	4	3	4	14

iv) 2000

	Sex	*Age*	Bayan	Badmaa	Delgerekh	Sharga	Zigmee	Ajarchan	Sha 99	Marcview	Bad 99	Total
Bayan	m	11	*	7	10	8	7	9	7	9	8	65
Badmaa	f	8	1	*	0	1	0	1	0	0	4	7
Delgerekh	f	4	0	0	*	0	0	0	1	3	0	4
Sharga	f	6	0	0	0	*	3	***0***	1	0	0	4
Zigmee	f	4	1	0	0	0	*	1	0	1	2	5
Ajarchan	f	7	2	0	0	***1***	0	*	0	0	0	3
Sha 99	f	1	0	0	0	0	0	0	*	0	1	1
Marcview	m	2	0	0	0	0	0	0	0	*	0	0
Bad 99	f	1	0	0	0	0	0	0	0	0	*	0
Total			4	7	10	10	10	11	9	13	15	89

c). Dominance hierarchy matrices of Margad's harem.
The winner of an interaction is down the side and the loser is along the top of the matrices.
i) 1999

	Sex	*Age*	Margad	Shuurga	Ireedui	Vetochka	Tsetseg	Evsel	Chotzj	Riska	Kharzaga	Naadam	Selenge	Total
Margad	m	5	*	19	23	18	17	18	22	17	22	17	22	195
Shuurga	f	9	3	*	1	0	1	0	0	3	5	1	2	16
Ireedui	f	5	1	0	*	0	0	1	1	4	6	1	0	14
Vetochka	f	9	0	0	0	*	0	0	0	0	1	1	0	2
Tsetseg	f	4	1	0	0	0	*	0	0	1	4	0	0	6
Evsel	f	2	0	0	0	0	0	*	0	0	1	0	1	2
Chotzj	f	3	0	0	0	0	0	0	*	0	2	0	0	2
Riska	f	9	0	0	0	0	0	0	0	*	0	0	0	0
Kharzaga	f	4	0	0	0	0	0	0	1	0	*	1	0	2
Naadam	f	1	0	0	0	0	0	0	0	0	0	*	1	1
Selenge	m	1	0	0	0	0	0	0	0	0	0	0	*	0
Total			5	19	24	18	18	19	24	25	41	21	26	240

ii) 2000

	Sex	*Age*	Margad	Riska	Shuurga	Ireedui	Tsetseg	Chotzj	Tse 99	Kharzaga	Sergelen	Evsel	Naadam	Selenge	Total
Margad	m	6	*	5	5	7	3	3	3	3	10	6	4	7	56
Riska	f	10	0	*	0	1	0	1	0	0	2	0	0	0	4
Shuurga	f	10	0	0	*	1	0	0	0	2	5	0	0	0	8
Ireedui	f	6	3	0	0	*	0	0	0	2	8	1	1	2	17
Tsetseg	f	5	0	0	0	0	*	0	0	0	3	0	0	0	3
Chotzj	f	4	0	0	0	0	0	*	0	0	6	0	0	3	9
Tse 99	f	1	0	0	0	0	0	0	*	0	0	0	0	0	0
Kharzaga	f	5	0	0	0	0	0	0	0	*	2	0	0	0	2
Sergelen	f	9	1	0	1	0	0	2	0	1	*	1	0	3	9
Evsel	f	3	0	0	0	0	0	0	0	0	0	*	2	0	2
Naadam	f	2	0	0	0	0	0	0	0	0	0	0	*	0	0
Selenge	m	2	0	0	0	0	0	0	0	0	0	0	0	*	0
Total			4	5	6	9	3	6	3	8	36	8	7	15	110

d). Dominance hierarchy matrices of Khaan's harem.

The winner of an interaction is down the side and the loser is along the top of the matrices.

i) 1998

	Sex	*Age*	Khaan	Shuurga	Naidvar	Belka	Svetlaya	Chotzj	Vetochka	Tsetseg	Riska	Adzargal	Evsel	Bernard	Ireedui	Balmoral	Total
Khaan	m	10	*	5	4	3	5	3	3	3	3	7	3	3	4	4	50
Shuurga	f	8	3	*	0	0	0	0	0	0	0	0	0	1	2	2	8
Naidvar	f	7	1	0	*	0	0	0	0	0	0	0	0	0	4	1	6
Belka	f	9	0	0	0	*	0	0	1	0	0	0	0	0	2	0	3
Svetlaya	f	8	0	0	0	0	*	0	0	0	1	0	1	0	0	0	2
Chotzj	f	2	0	0	0	0	0	*	0	0	0	1	0	0	0	0	1
Vetochka	f	8	0	0	0	0	0	0	*	0	0	0	0	0	1	0	1
Tsetseg	f	3	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0
Riska	f	8	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0
Adzargal	m	2	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0
Evsel	f	1	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0
Bernard	m	1	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0
Ireedui	f	4	1	0	0	0	0	0	0	0	0	0	0	0	*	1	2
Balmoral	m	1	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0
Total			5	5	4	3	5	3	4	3	4	8	4	4	13	8	73

ii) 1999

	Sex	*Age*	Khaan	Shuurga	Belka	Svetlaya	Balmoral	Selenge	Ireedui	Total
Khaan	m	11	*	19	11	11	13	10	13	77
Shuurga	f	9	1	*	0	0	0	0	1	2
Belka	f	10	0	0	*	0	0	0	0	0
Svetlaya	f	9	0	0	0	*	0	0	0	0
Balmoral	m	2	0	0	0	0	*	0	0	0
Selenge	m	1	0	0	0	0	0	*	0	0
Ireedui	f	5	0	0	0	0	0	0	*	0
Total			1	19	11	11	13	10	14	79

e). Dominance hierarchy matrices of Ares' harem.

	Sex	*Age*	Ares	Khalioen	Tsagaan	Ayush	Zeerd	Caborg	Total
Ares	m	9	*	7	7	6	6	6	32
Khalioen	f	4	0	*	1	2	4	1	8
Tsagaan	f	8	0	0	*	0	2	1	3
Ayush	f	4	0	0	0	*	0	1	1
Zeerd	f	4	0	0	0	0	*	0	0
Caborg	f	1	0	0	0	0	0	*	0
Total			0	7	8	8	12	9	44

Appendix X. Pearson's correlation coefficients and their significance for factors affecting the dominance of horses within each harem. Aggression is the number of aggressive acts hour^{-1} of each horse.

a) Paritet's harem

Year	Factor	Position		Aggression		Age	
		r	p	r	p	r	p
1998	Aggression	-0.35	0.445				
	Age	-0.74	0.058	0.32	0.485		
	Tenure	-0.55	0.197	0.20	0.668	0.93	0.002
1999	Aggression	-0.86	0.001				
	Age	-0.54	0.084	0.47	0.14		
	Tenure	-0.80	0.003	0.60	0.051	0.47	0.149
2000	Aggression	-0.69	0.006				
	Age	-0.78	0.001	0.52	0.058		
	Tenure	-0.87	<0.001	0.55	0.042	0.69	0.006
All years	Aggression	-0.43	0.014				
	Age	-0.64	<0.001	0.41	0.021		
	Tenure	-0.73	<0.001	0.47	0.006	0.64	<0.001

b) Bayan's harem

Year	Factor	Position		Aggression		Age	
		r	p	r	p	r	p
1998	Aggression	-0.61	0.201				
	Age	-0.47	0.351	0.2	0.704		
	Tenure						
1999	Aggression	-0.75	0.031				
	Age	-0.71	0.047	0.8	0.009		
	Tenure	-0.85	0.008	0.6	0.091	0.80	0.018
2000	Aggression	-0.85	0.004				
	Age	-0.84	0.004	0.9	0.003		
	Tenure	-0.69	0.04	0.6	0.089	0.91	0.001
All years	Aggression	-0.58	0.004				
	Age	-0.72	<0.001	0.5	0.01		
	Tenure	-0.58	0.004	0.6	0.002	0.59	0.003

c) Margad's harem

Year	Factor	Position		Aggression		Age	
		r	p	r	p	r	p
1999	Aggression	-0.74	0.009				
	Age	-0.54	0.084	0.17	0.613		
	Tenure	-0.21	0.528	-0.23	0.501	0.80	0.003
2000	Aggression	-0.67	0.018				
	Age	-0.73	0.007	0.40	0.192		
	Tenure	-0.56	0.061	0.10	0.76	0.67	0.017
All years	Aggression	-0.64	0.001				
	Age	-0.63	0.001	0.30	0.164		
	Tenure	-0.38	0.072	-0.02	0.94	0.74	<0.001

d) Khaan's harem

Year	Factor	Position		Aggression		Age	
		r	p	r	p	r	p
1998	Aggression	-0.74	0.002				
	Age	-0.76	0.002	0.64	0.014		
	Tenure	-0.41	0.144	0.28	0.327	0.81	<0.001
1999	Aggression	-0.65	0.114				
	Age	-0.80	0.029	0.50	0.257		
	Tenure	-0.54	0.211	0.43	0.331	0.87	0.012
All years	Aggression	-0.46	0.038				
	Age	-0.73	<0.001	0.47	0.033		
	Tenure	-0.47	0.03	0.35	0.116	0.84	<0.001

e) Ares' harem

Year	Factor	Position		Aggression	
		r	p	r	p
1998	Aggression	-0.94	0.005		
	Age	-0.79	0.06	0.75	0.087

Appendix XI. Flies caught in sticky and water traps, 1998

Description	Number caught	
	Water	Sticky
Fly <1mm	15	38
Red eye, black and grey striped abdomen fly	6	15
Gold abdomen fly	1	3
Big (1.5cm) hairy fly, striped thorax and abdomen	1	1
Brown flies		2
Long bodied flies	2	
1cm grey fly, striped abdomen with brown long 'tail'		1
5mm gray thorax fly		1
5mm grey, brown eye fly		1
Black/grey fly, red/brown eyes		1
Half red abdomen fly (?)		1
Orange abdomen red eye fly		1
Red eye, white abdomen fly	1	
Small black fly (5mm)	1	
Speckled wing delta fly	1	
Mosquito		1
Hoverfly		1
Dragonfly	1	
Grasshopper	1	4
Beetle	3	
Wasp	2	1
Bee	2	
Flying ant		2
Butterfly	2	
Aphid	1	

Appendix XII. Pearson's correlation coefficients between different environmental variables affecting the number of flies on a horse. P values are given underneath the correlation coefficient (r).

	Month	Hour	Wind speed	Temperature
Hour	0.14			
	p = 0.019			
Wind speed	0.13	0.07		
	p = 0.038	p = 0.248		
Temperature	-0.4	0.12	-0.06	
	p = <0.0001	p = 0.043	p = 0.289	
Cloud cover	-0.28	-0.14	-0.05	-0.14
	p = <0.0001	p = 0.025	p = 0.397	p = 0.025